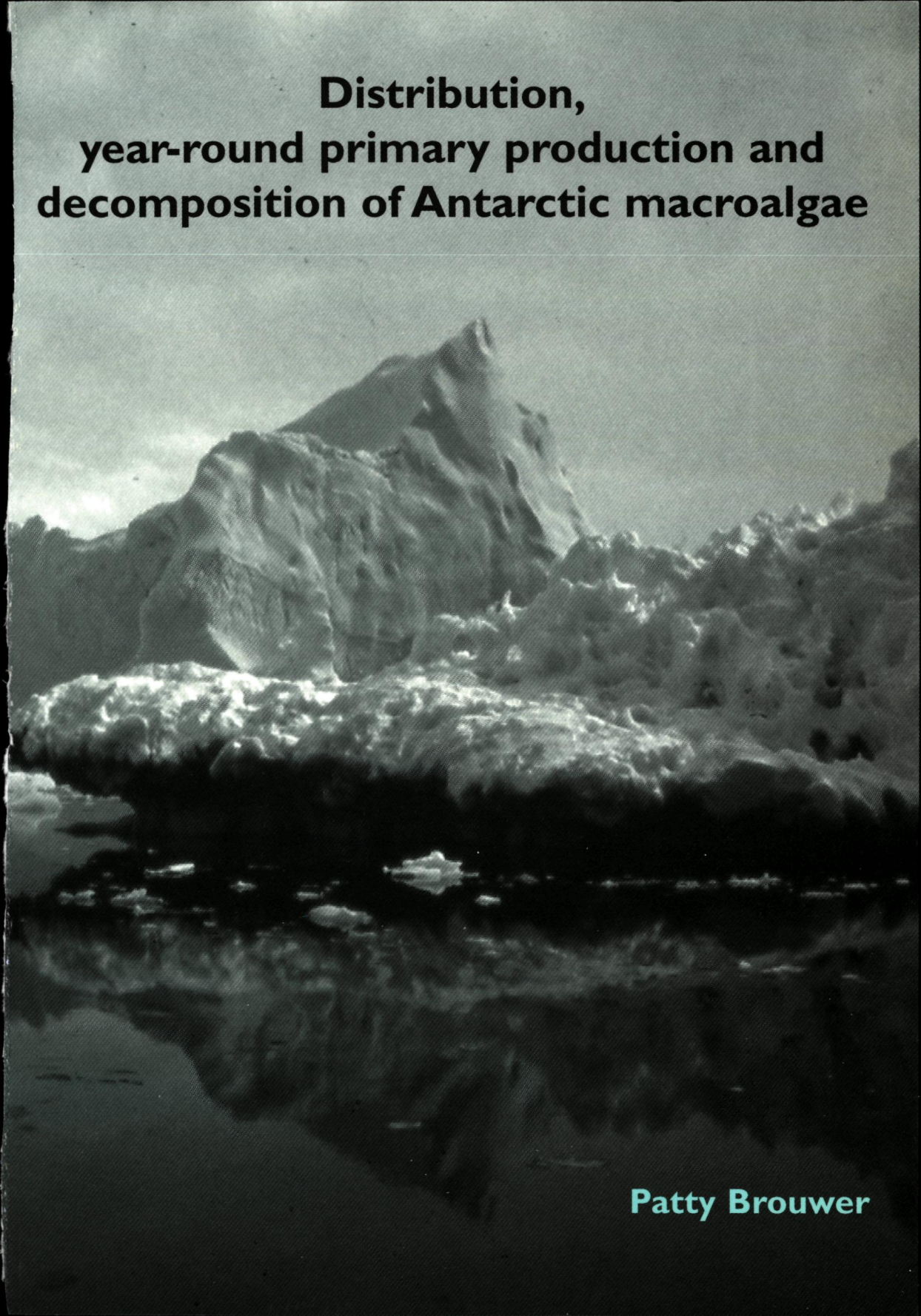
Distribution, year-round primary production and decomposition of Antarctic macroalgae



Patty Brouwer

Distribution, year-round primary production and decomposition of Antarctic macroalgae

een wetenschappelijke proeve op
het gebied van de Natuurwetenschappen

PROEFSCHRIFT

ter verkrijging van de graad van doctor
aan de Katholieke Universiteit Nijmegen,
volgens besluit van het College van Decanen
in het openbaar te verdedigen
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des namiddags om 3 30 uur precies

door

Patricia Elisabeth Mathea Brouwer

geboren 21 februari 1964
te Heerlen

Promotores:	Prof. Dr. P.H. Nienhuis
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Prof. Dr. G. van der Velde (VU, Brussel)

"Without algae there would be no life on earth. The oceans would be sterile and the land uncolonised" - Wall inscription, Kew Gardens, London

Voor mijn ouders

GOA

NWO

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Voorwoord

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Patty

Contents

General introduction

Antarctica has been unexplored for a long time The first biological expeditions to this continent date back to 1817 with Gaudichaud, Bory, Montagne, Hooker and Harvey (Godley 1965, Papenfuss 1964) They used remote sampling methods for macroalgae parts of dredged macroalgal material were brought up to the surface A lot of macroalgae were found drifting in open water or found washed ashore The pioneer Skottsberg (1907, 1941) was the first to study the ecology of the intertidal and shallow littoral, examining marine macroalgae of sub-Antarctic islands All these early expeditions mainly resulted in taxonomic studies and biogeographic investigations, which formed the foundation for later studies of the marine flora and fauna Recently, the Antarctic marine flora has been estimated at more than 120 species (Clayton 1994) This might be an underestimation as new species are still being found and many places are still unexplored However, the number of species will never equal those of temperate and tropical regions, as numbers decrease drastically towards higher latitudes Only seven species were found above 76°S (Zaneveld 1966) One of the most recent expeditions for systematic collections of macroalgae went to Terra Nova Bay, between 74°31'S and 74°55'S, where 17 species were recorded (Cormaci et al 1992)

The last decade more information became available about biogeographical relationships (Wiencke 1996 and references therein) and the ecophysiology of Antarctic macroalgae, obtained from a large number of isolated and cultivated species (Clayton and Wiencke 1986, Wiencke 1988) The biogeographical distribution area of a macroalga is primarily defined by temperature regimes required for reproduction, growth and survival (Breeman 1988, 1990, van den Hoek 1982a, 1982b) Temperature requirements of Antarctic species were mainly studied by Wiencke et al (1993, 1994) and Wiencke and tom Dieck (1989, 1990) Results showed a very strong adaptation to low temperatures in endemic species (Wiencke et al 1994), of which some show temperature demands comparable with other Antarctic cold-temperate macroalgae (Wiencke and tom Dieck 1990) The low temperature adaptation is also reflected in the photosynthetic level, although optimal temperatures for photosynthesis are above the prevailing water temperatures (Wiencke et al 1993) The species studied by Wiencke et al (1993) had low light demands and photosynthesis was light-saturated at irradiance levels typical for low light-adapted macroalgae

Field observations and *in situ* measurements of photosynthesis in Antarctica are generally lacking in literature Species lists are scarce and incomplete Zonation patterns of Antarctic macroalgae are described but mainly based on qualitative observations (Amsler et al 1990, Chung et al 1994, Kloser et al 1994, Zielinski

1990), while reports on estimates of biomass are very rare (Richardson 1979, White and Robins 1972) This is in contrast to studies of macroalgal biomass in sub-Antarctic waters (Attwood et al 1991, Delepine 1976, Lawrence 1986) The inaccessibility of the Antarctic region and the necessity of SCUBA diving for *in situ* research are probably the main reasons for the limited information available The only *in situ* photosynthetic study on Antarctic macroalgae dates from 1973-1975 (Drew and Hastings 1992), while at the start of this project photosynthetic studies on fresh macroalgal material collected in the field and studied in laboratories were also scarce (Drew 1977, Drew and Hastings 1992, Gutkowski and Maleszewski 1989)

The aim of this thesis is first of all to gain insight in the functioning of some large Antarctic marine benthic algae under field conditions, and secondly to validate the results of laboratory studies in the field.

The present project, which was carried out at Signy Island (60°42'S, 45°36'W, Fig 1.1), was part of the Netherlands Antarctic Research Programme of 1990-1994, funded by the Geosciences Foundation (GOA) of the Netherlands Organization for Scientific Research (NWO) Connections with the British Antarctic Survey, via Dr AHL Huiskes, created the opportunities for working at the Signy Island field station Signy Island is one of the South Orkney Islands, which according to the biogeographical scheme of Hedgpeth (1969) belong to the sub-regio Western Antarctic, comprising of the Antarctic Peninsula and the Scotia Arc. Signy Island is a small island of approximately 5 by 7 km Due to the position of the British Antarctic Survey base on the east side of the island at Factory Cove, the main research area was confined to Borge Bay Borge Bay covers about 2 km^2 and consists of a series of inlets and shallow embayments The maximum depth of Borge Bay is roughly 30 m, with a mean depth of 10 m The composition of the bottom ranges from rock to fine sand and determines the macroalgal distribution (Richardson 1979) Depths deeper than 30 m are found towards Orwell Bight and the east side of Outer Island There is free exchange of water between Borge Bay and the Orwell Bight, since the bay entrance is unrestricted and has no underwater sill.

The study of marine ecology at Signy Island has a relatively long history A monitoring programme started as early as 1969, measuring temperature, salinity, chlorophyll, nitrate, nitrite, phosphate, silicate and ammonia of the seawater (Clarke et al. 1988) The first marine ecological research on macroalgal species at Signy Island was carried out from December 1962 to April 1965, briefly mentioning the macroalgae being present (Price and Redfearn 1968) Only few macroalgal studies followed at Signy Island (Drew 1977, Drew and Hastings 1992, Richardson 1979, White and Robins 1972)

In 1991 an intensive *in situ* study was started, which forms the basis of this thesis The results form a valuable link between the descriptive studies already available of Antarctic macroalgae and the laboratory work carried out on cultured

macroalgae. During two field periods, from November 1991 till April 1992 and from November 1992 till November 1993, the macroalgal zonation patterns, productivity of

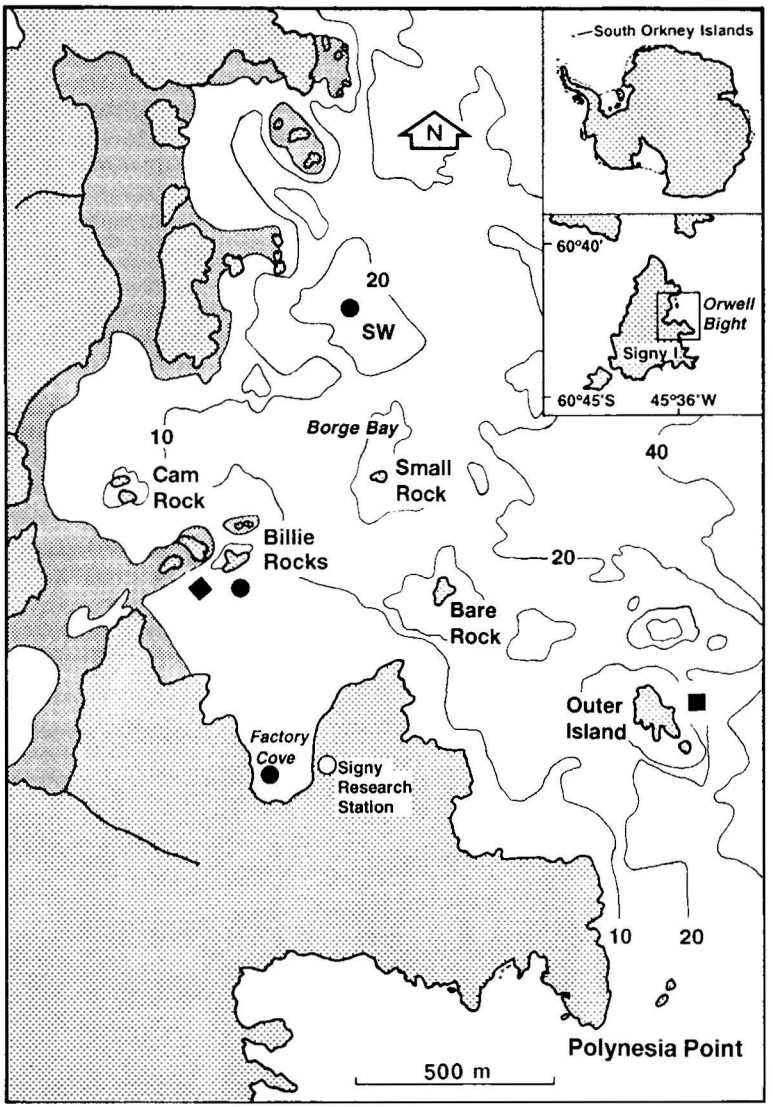

Figure 1.1. Map showing the location of the South Orkney Islands, Signy Island, and the study area. Sites of the zonation pattern study: Outer Island and Polynesia Point (exposed), Billie Rocks, Cam Rock, Small Rock and Bare Rock (sheltered) (Chapter 2); location of the incubation experiments (●) (Chapter 3, 4 and 5); location of the growth experiment of *Himantothallus grandifolius* (■) (Chapter 5); location of the decomposition experiment (◆) (Chapter 6); *SW* marks the seawater sampling site and the hollow of the seabed where accumulations of detached macroalgae occurred; the *light dotted areas* are supralittoral and terrestrial areas; the *dark dotted areas* are shallows and scattered rocks; depth in metres (m)

several dominant species and the decomposition rate of one of the dominant species were examined First a detailed study on the distribution and the zonation patterns of the sublittoral macroalgal communities was started of which the results are presented in **Chapter 2** A complete species list is given for Signy Island and data on standing crop and percentage cover are used in relation to depth and exposition of two sites to collect information on the distribution and zonation pattern Also the influence of environmental variables on the species composition is quantified

From the first macroalgal biomass estimations carried out in the sheltered area of Borge Bay (at Billie Rocks, Fig 1 1), the three most important macroalgae were selected for the *in situ* photosynthetic measurements in different seasons Of the Phaeophytes *Desmarestia anceps* Montagne and *Himantothallus grandifolius* Skottsberg were chosen for their difference in morphology They are both the most abundant species in biomass *Desmarestia anceps* is a bushy macroalga forming branches, while *Himantothallus grandifolius* is a kelp-like macroalga with long and flat laminae Of the Rhodophytes *Myriogramme mangini* (Gain) Skottsberg was chosen, the most abundant red macroalga in biomass at Billie Rocks, which mainly grows as understory species and in rock crevices By determining the photosynthetic characteristics of these macroalgae our knowledge of macroalgal photosynthesis under natural field circumstances improved greatly. Annual production rates were calculated using the seasonal P-I curves defined for each species in combination with predicted daily irradiance levels to a water depth of 25 m In **Chapter 3** the oxygen production rates of *Desmarestia anceps* are given, including details of the self-registering incubation chambers used for the experiments with the three selected species Whether seasonal variation in maximal production and photosynthetic efficiencies can be related to changes in chlorophyll *a* without including other pigments is discussed **Chapter 4** summarizes the measurements carried out with *Myriogramme mangini*, and includes year-round irradiance levels measured under water till a depth of 25 m A classification of the water types is given in relation to the predicted annual course of daily net production In **Chapter 5** the results of the experiments with *Himantothallus grandifolius* are shown. A comparison and evaluation is made between results obtained from photosynthetic measurements, using the self-registering incubation chambers, and growth rates obtained with a marking method CNP contents and chlorophyll *a* content were determined in order to explain differences in growth rates at two light regimes

To close the circle of productivity and decay, in **Chapter 6** the decomposition rate of *Desmarestia anceps* was determined in order to assess the timescale over which nutrients become available again for the marine ecosystem

In **Chapter 7**, the general discussion, a synthesis of distribution, production and decomposition of Antarctic macroalgae is given

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Biomass, cover and zonation pattern of sublittoral macroalgae at Signy Island, South Orkney Islands, Antarctica

Patty EM Brouwer, Noel (E)FM Geilen, Niek JM Gremmen, Frances van Lent

Abstract

Antarctic macroalgae have been studied taxonomically and biogeographically, but vegetational zonation patterns are still described intuitively Quantitative studies on the macroalgal vegetation at Signy Island, Antarctica, are scarce The aims of this study were to provide a more complete species list, to collect information on the distribution and zonation pattern of the algae by studying standing crop and percentage cover of the macroalgae in relation to depth and site, and to quantify the influence of environmental variables on the species composition of macroalgal communities Transects at two rocky sites, one sheltered and one exposed, were studied in detail using both a photographic and a harvest sampling method Thirty six species were identified Both the number of species and macroalgal biomass were low compared with sub-Antarctic regions The vertical zonation found was an ice-abraded zone characterized by *Iridaea cordata*, a zone 5 to 14 m depth dominated by *Desmarestia anceps* and *Desmarestia menziesii* and a zone 15 to 25 m characterized by *Himantothallus grandifolius* Of the four environmental variables studied (depth, substratum, slope, exposure) only depth and substratum were significantly related to the species composition of the algal vegetation No species were found with an optimum at depths greater than 20 m and the lowest depth of occurrence for *Himantothallus grandifolius* was predicted at 35 m A consistent shift was found between the two sites studied sample plots of the sheltered site corresponded with plots roughly 1 to 2 m deeper at the exposed site Depth-response models of the macroalgae indicated a higher probability of occurrence for *Desmarestia anceps*, *Himantothallus grandifolius* and Rhodophyta towards shallower depths at the more sheltered site The probability of finding *Desmarestia anceps* deeper than 29 m is nil, while the possibility of finding *Himantothallus grandifolius* is still 20% at 29 m

Important factors in explaining the growth of macroalgae higher in the sublittoral at the sheltered site might be the light conditions and ice scouring at the start of the growing season. In summer, differences in exposure and biological factors might be of more importance in explaining the biomass differences in macroalgae between the two sites.

Introduction

The taxonomy and distribution of the flora of the Southern Ocean have been studied from the very beginning of Antarctic explorations (reviewed in Heywood and Whitaker 1984, and updated by Chung et al. 1994, Cormaci et al. 1992, Dayton 1990, Klöser et al. 1994, Moe and Silva 1989). Macroalgal communities in Antarctica have been classified, more or less intuitively, into an ice-abraded zone of poorly developed vegetation in the shallow sublittoral, a zone in the central sublittoral dominated by *Desmarestia anceps* and *Desmarestia menziesii* and a zone of *Himantothallus grandifolius* at greater depth (Dayton 1990, reviewed in Heywood and Whitaker 1984).

Signy Island (lat. 60°42'S, long. 45°36'W), one of the South Orkney Islands (Fig. 1.1), is situated in the maritime Antarctic. The climate of Signy Island is described by Holdgate (1967). In summer daylight may last for up to 19 h in December, with a minimum winter daylength of 6 h in June. Seawater temperature varies from -1.8°C in winter to about +0.3°C in summer, salinity is constant (33.9 ‰ ± 0.5) apart from occasional slightly lower surface values caused by melt water (Clarke et al. 1988). Sea ice is present for an average of 140 days each year, with a large year to year variation (Clarke et al. 1988).

Previous studies on the distribution of macroalgae at Signy Island consisted of qualitative observations of benthic macroalgae (Price and Redfearn 1968), preliminary estimates of total macroalgal biomass (White and Robins 1972), and a study of the distribution of *Desmarestia* sp. and *Himantothallus grandifolius* in relation to depth and substratum (Richardson 1979). Physiology of Antarctic macroalgae has been studied, with particular emphasis on photosynthesis, respiration, plant growth and tissue composition by Drew (1977) and Drew and Hastings (1992). Species lists of the sublittoral macroalgae of Signy Island as reported in the literature are incomplete, for the most abundant Rhodophyta have often been grouped into a single broad taxon. The largest published number of species at Signy Island is nineteen (Price and Redfearn 1968).

A complete description of sublittoral vegetations of the Antarctic had yet to be undertaken and therefore we report in this paper the results of a detailed study of the shallow water macroalgal communities of Signy Island, the northern limit of the Antarctic Peninsular Region. The aims of our study were firstly to provide a more

complete species list of the Signy Island sublittoral macroalgae and secondly to collect information of the distribution and zonation pattern of the algae by studying the standing crop and percentage cover of the macroalgae in relation to depth and a number of sites. Finally, we wanted to quantify the influence of exposure, depth and substratum on the species composition of the macroalgal communities.

Materials and methods

Study area

The study was carried out in Borge Bay and the adjoining part of Orwell Bight (Fig. 1.1) from December 1991 to March 1992, and December 1992 to November 1993. The six sampling sites could be classified into two groups on the basis of maximum depth at the sampling site, estimated angle of open water influencing the sampling site, and the distance from the sampling site to the nearest land (Table 2.1). The first, more exposed, group comprised the seaward area of Outer Island, situated at the mouth of Borge Bay, and Polynesia Point, both directly exposed to the wave action and currents from Orwell Bight and heavily affected by ice to all depths. The second group comprised the landward sides of Billie Rocks, Cam Rock, Small Rock and Bare Rock, which are situated in the sheltered shallow landward area of Borge Bay. Ice scouring occurs at all sites in the uppermost metres. Pack ice and smaller icebergs regularly drift into Borge Bay and Factory Cove. Large icebergs usually run aground before entering Borge Bay, and may influence the benthic communities at Outer Island and Polynesia Point. The main wind direction for Signy Island during the period of January 1993 to November 1993 was 275° (westerly).

Table 2.1. Characteristics of the sampling sites at Borge Bay. Depth is the maximum depth at the sampling site; angle is the total angle of open water influencing the sampling site; distance is the distance from the sampling site to the nearest land

Sites		Depth (m)	Angle (°)	Distance (km)
Exposed group:	Outer Island	38	210	5-500
	Polynesia Point	24	165	5-500
Sheltered group.	Billie Rocks	12	135	0.2-0.5
	Cam Rock	10	180	0.2-0.3
	Small Rock	12	200	0.3-0.6
	Bare Rock	12	135	0.2-0.8

Data collection

During a number of SCUBA dives, collections of macroalgae were made at the six sites from depths down to 29 m below mean low water (MLW) for providing a more complete species list of the Signy Island sublittoral macroalgae. As diving conditions at below zero temperatures are not optimal it is expected that very small and encrusting species were not exhaustively collected. All macroalgae collected were identified whilst still alive. Photographs were taken of any unknown species and representative specimens were stored in a herbarium for later identification.

At two sites, the sheltered Billie Rocks and the exposed Outer Island, a detailed study of the cover and biomass distribution of the macroalgae was made. Along transects perpendicular to the shore sample plots were chosen at 3 m depth intervals starting at 2 m below MLW. At Outer Island the transect ran to a depth of 29 m, but at Billie Rocks the deepest sampling site was at 11 m below MLW as the maximum depth reached was 12 m. For each plot the following characteristics were measured or estimated:

- depth (m) related to mean low water level (MLW);
- slope of the substratum, in degrees;
- type of substratum, classified on a 6-point scale: 1 = solid rock; 2 = solid rock and boulders larger than 1 m; 3 = solid rock and boulders smaller than 1 m; 4 = boulders of 0.5 - 1 m; 5 = boulders and pebbles smaller than 0.5 m; 6 = pebbles and sediment.

Quadrats (50 x 50 cm) were placed randomly at each depth along the transect. To reduce worktime under water and to protect the area from too severe damage, colour transparancies were taken from the quadrats for determining percentage cover of the species in addition to a sampling method where the quadrat area was cleared of macroalgae. The methods for determining sampling unit size and sample number are numerous and recommendations as to quadrat size as quadrat number vary in the literature (de Wreede 1985). In general, taking as many samples as possible is advised (Green 1979). Our choice of the quadrat size was based on the ability to recognize the species on transparencies and keeping the damaged area to a minimum.

For determination of the standing crop at each depth, all macroalgae attached to the substratum within seven 50 x 50 cm quadrats were collected by removing them from the rock substratum as completely as possible. Samples were transported in buckets or insulated boxes with seawater and stored in the laboratory in containers with a continuous flow of seawater pumped directly from Factory Cove. For five quadrats the material was subsequently sorted to the species level. Two quadrats were sorted to the species level for only the brown macroalgae while the red macroalgae were grouped as Rhodophyta. Wet weight (WW) of the algae was

measured as soon as possible, after removing adherent water with blotting paper. Sub-samples were dried at 60°C for at least 48 hours to obtain a constant dry weight (DW).

Species cover was estimated on 35 mm colour transparencies taken from 7 to 13 quadrats per site per depth (depending on camera use and results after developing the film) using Nikonos IV and V cameras equipped with electronic flashes. This method under-estimates the cover of macroalgae in the understory. It was not possible to identify the red macroalgae at the species level on the transparencies. They were therefore classified simply as Rhodophyta.

Data analysis

Biomass and cover data of the most common species of Phaeophyta and the total Rhodophyta for each quadrat were analysed for the relationship with the environmental variables depth and site by using the analysis of variance option in SYSTAT (Wilkinson 1990). Results from corresponding depths of the two sites were used.

A classification of the sample sites based on species composition was made using TWINSPAN (Hill 1979). Standing crop of each species was calculated from lumping the five replicate 50 x 50 sample plots from 10 depth levels at Outer Island and 4 levels at Billie Rocks Cutlevels (g DW) in the analysis were: 1, (0-5), 2, (5-10), 3, (10-100); 4, (100-250); 5, (250-500), 6, (500-1000); 7, (1000-1500); 8, (1500-2000).

The relation between species composition and site characteristics was analysed by canonical correspondence analysis (CCA, ter Braak 1987), using the same standing crop data as in the classification. The programme used was CANOCO, version 3.12 (ter Braak 1988, 1990), using the standard options. Significance of the relation between environmental variables and the position of the sample plots on the first ordination axis was tested using Monte Carlo permutation tests (Manly 1990) with 99 permutations and a significance level of 5%

Logistic regression (ter Braak and Looman 1987) was used to predict the probability of species presence in any random quadrat as a function of an environmental factor (Austin et al 1984), which in this study was water depth. Presence-absence scores were based on the biomass as well as the cover data taken at Billie Rocks and Outer Island in order to minimize artefacts due to methodological differences and seasonal effects. The following model was used for the species response to the environmental variable (ter Braak and Looman 1987).

$$p = [\exp (b_0 + b_1 x + b_2 x^2)]/[1 + \exp (b_0 + b_1 x + b_2 x^2)],$$

where x is the value for an environmental variable, b_0 is a constant, b_1 and b_2 are

coefficients, p is the probability of the species being present. This model describes a bell shaped Gaussian response curve. When b_1 does not differ significantly from zero, no significant influence of the environmental variable on the presence of the species is detected. When b_2 is not significantly different from zero, the response curve is sigmoid. Whether b_1 and b_2 differ significantly from zero is determined by a t-test ($p<0.05$). In the case of a Gaussian response function the optimum (u), tolerance (t) and maximum probability of occurrence (p_{max}) can be calculated using the following equations (ter Braak and Looman 1987):

$$u = -b_1/(2b_2)$$
$$t = 1/\sqrt{(-2b_2)}$$
$$p_{max} = p(u) = [\exp(b_0 + b_1 u + b_2 u^2)]/[1 + \exp(b_0 + b_1 u + b_2 u^2)].$$

Results

Abundance of macroalgae

A total of 36 species was identified in the study area (Table 2.2), of which 24 species were found within the quadrats.

Although the macroalgal population at Outer Island reached higher mean biomass values (Figs. 2.1 and 2.2) than the population at Billie Rocks, no significant differences between biomass figures at corresponding depths at Outer Island and Billie Rocks were found (Table 2.3). The biomass of *Himantothallus grandifolius* increased significantly with depth at corresponding depths of Outer Island and Billie Rocks ($p<0.01$) (Table 2.3, Fig. 2.1). *Himantothallus grandifolius* showed significantly more cover at Billie Rocks than at the same depths of Outer Island ($p<0.01$, Fig. 2.3), but no significant differences between Outer Island and Billie Rocks were found in the total cover of the macroalgae (Table 2.3). In contrast with the biomass data, the percentage cover of *Desmarestia anceps*, *Himantothallus grandifolius* and the overall percentage cover by macroalgae did increase significantly with depth. Again, only *Himantothallus grandifolius* showed significantly higher cover at Billie Rocks than at Outer Island. The 'site x depth' interaction ($p<0.05$) can be explained from the slower increase in percentage cover of *Himantothallus grandifolius* with depth at Outer Island compared with Billie Rocks (Table 2.3).

At a depth of 11 m, a maximum biomass of 0.24 kg DW m^{-2} (1.25 kg WW m^{-2}) was found for *Himantothallus grandifolius*, 1.00 kg DW m^{-2} (5.66 kg WW m^{-2}) for *Desmarestia anceps* and 0.46 kg DW m^{-2} (1.85 kg WW m^{-2}) for *Desmarestia menziesii*, giving a total maximum biomass of these brown macroalgae of 1.7 kg DW m^{-2} (8.8 kg WW m^{-2}) at Outer Island. Unpublished data for Bare Rock from this study,

include a biomass for *Desmarestia anceps* of 3.3 kg DW m^2 (20.0 kg WW m^2) at 5 m depth.

Table 2.2. Species list of macroalgae found at the six locations studied at Signy Island

Species	Abbreviation (a)
Chlorophyta	
Enteromorpha bulbosa (Suhr) Montagne	-
Monostroma hariotii Gain	-
Lambia antarctica (Skottsberg) Delepine*	-
Phaeophyta	
Adenocystis utricularis (Bory) Skottsberg	Ade ut
Ascoseira mirabilis Skottsberg	Asc mi
Desmarestia anceps Montagne	Des an
Desmarestia antarctica Moe *et* Silva	-
Desmarestia confervoides (Bory) Ramirez *et* Peters*	-
Desmarestia menziesii J. Agardh	Des me
Halopteris obovata (J. D. Hooker *et* Harvey) Sauvageau*	-
Himantothallus grandifolius Skottsberg	Him gr
Phaeurus antarcticus Skottsberg*	-
Rhodophyta	
Ballia callitricha (C Agardh) Kutzing	-
Callophyllis sp.	Cal sp
Curdiea racovitzae Hariot	Cur ra
Delesseria lancifolia (J. D. Hooker) J. Agardh*	Del la
Delesseria salicifolia Reinsch*	Del sa
Delesseria sp.*	Del sp
Delisea pulchra (Greville) Montagne*	Del pu
Georgiella confluens (Reinsch) Kylin	Geo co
Gigartina papillosa (Bory) Setchell *et* Gardner*	-
Gigartina skottsbergii Setchell *et* Gardner	Gig sk
Hymenena laciniata (J. D. Hooker *et* Harvey) Kylin*	Hym la
Hymenocladiopsis crustigena Moe*	Hym cr
Iridaea cordata (Turner) Bory	Iri co
Kallymenia antarctica Hariot*	Kal an
Myriogramme mangini (Gain) Skottsberg	Myr ma
Notophycus fimbriatus Moe*	-
Palmaria decipiens (Reinsch) Ricker	-
Pantoneura plocamioides Kylin*	Pan pl
Phycodrys antarctica (Skottsberg) Skottsberg	Phy an
Phyllophora appendiculata Skottsberg	Phy ap
Picconiella plumosa (Kylin) J De Toni*	Pic pl
Plocamium cartilagineum (Linnaeus) Dixon	Plo ca
Porphyra plocamiestris Ricker	-
Sarcodia montagneana (J D. Hooker *et* Harvey) J. Agardh	Sar mo

*. Species not recorded for Signy Island before,
a As used in Figs. 2 1-2 5,
- = not used in further analysis

Table 2.3. ANOVA table of macroalgal standing crop (g DW m^{-2}) (*top*, n = 7) and cover data (%) (*bottom*, n = 7-13) for comparable depths at Billie Rocks and Outer Island; F-values are shown. Significant effects are denoted: * = p<0.05, ** = p<0.01, *** = p<0.001, ns = not significant. Abbreviations as in Table 2.2

	Him gr	Des an	Des me	Rhodophyta	Total biomass
Depth	5.67**	1.06 ns	0.11 ns	0.65 ns	2.03 ns
Site	1.22 ns	1.08 ns	1.76 ns	3.97 ns	1.96 ns
Depth x site	0.63 ns	2.60 ns	1.53 ns	0.56 ns	2.37 ns
	Him gr	**Des an**	**Des me**	**Rhodophyta**	**Total cover**
Depth	31.60***	10.19***	2.65 ns	2.59 ns	11.75***
Site	9.07**	0.17 ns	1.74 ns	2.47 ns	0.02 ns
Depth x site	3.89*	0.78 ns	2.08 ns	2.70 ns	0.42 ns

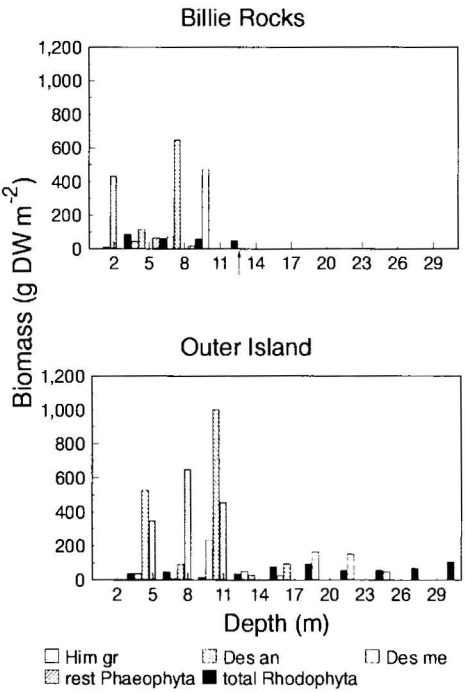

Figure 2.1. Average biomass values (g DW m^{-2}) of macroalgae at Outer Island and Billie Rocks (n = 7). Standard deviations not shown. 'Rest Phaeophyta' = total biomass of un-specified brown macroalgae (g DW m^{-2}). 'Total Rhodophyta' = total biomass of Rhodophyta (g DW m^{-2}). ↑: Indicates maximum depth at Billie Rocks. Abbreviations are given in Table 2.2

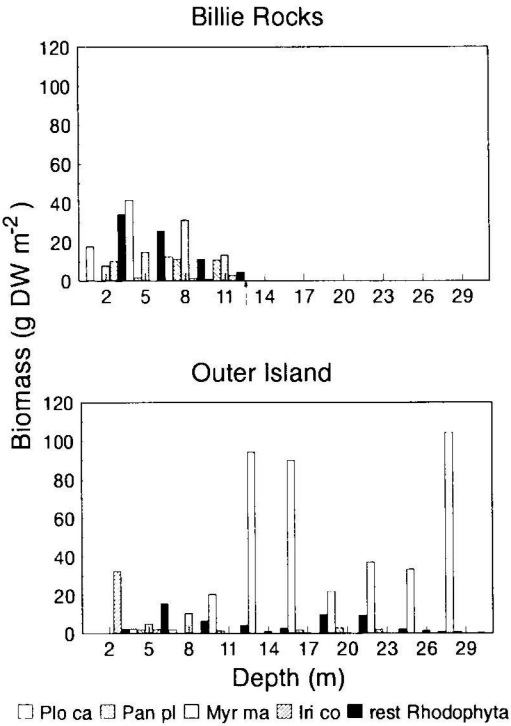

Figure 2.2. Average biomass values (g DW m^{-2}) of the most abundant Rhodophyta at Outer Island and Billie Rocks (n = 5). Standard deviations not shown. 'Rest Rhodophyta' = total biomass of unspecified red macroalgae (g DW m^{-2}). ↑: Indicates maximum depth at Billie Rocks. Abbreviations are given in Table 2.2

Classification

Classification of the lumped species biomass data from Outer Island and Billie Rocks using TWINSPAN, yielded five groups (Table 2.4). Cluster A consisted of the exposed plots of medium depth dominated by *Desmarestia anceps*, *Himantothallus grandifolius* and *Plocamium cartilagineum*. *Hymenena laciniata* was only found in cluster A. Cluster B contained the exposed and deep plots with *Himantothallus grandifolius* and *Plocamium cartilagineum* as dominant species, and without *Desmarestia anceps*. Cluster C consists of shallow and sheltered plots (all at Billie Rocks) with the highest number of species. *Ascoseira mirabilis* and *Callophyllis* sp. are restricted to this group. Shallow and usually exposed plots, dominated by *Desmarestia anceps* and *Desmarestia menziesii*, form cluster D. The very poor species site at the shallow end of the exposed Outer Island transect was separated from all other sites in cluster E. This was the only place where *Adenocystis utricularis* was found.

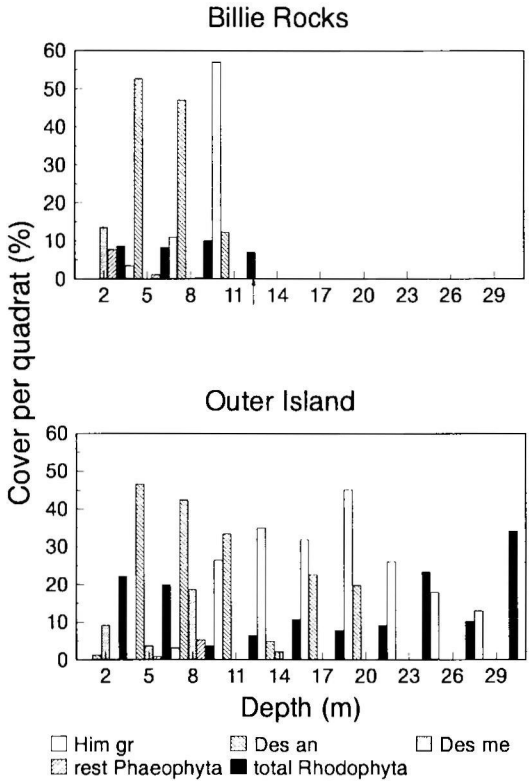

Figure 2.3. The average percentage cover per quadrat at Outer Island and Billie Rocks (n = 7-13). Standard deviations are not shown. 'Rest Phaeophyta' = total % cover of un-specified Phaeophyta. 'Total Rhodophyta' = total % cover of Rhodophyta. ↑: Indicates maximum depth at Billie Rocks. Abbreviations are given in Table 2.2

Ordination

The canonical correspondence analysis (CCA) of the biomass data showed depth and substratum to be significantly related to species composition, but did not indicate a relation between biomass and exposure or slope of substratum. The result of the CCA using depth and substratum as explanatory variables is illustrated in Fig. 2.4. The eigenvalues of the first two ordination axes are 0.61 and 0.15. The first axis explains 25%, and the two axes together explain 32% of the species variance, while explanation of the species-environment relation is 80 and 100%, respectively. Projection of the position of the sites on the arrow representing depth, showed a slight, but consistent shift of the plots of the Outer Island series relative to the Billie Rocks series. Sample plots of the Billie Rocks series corresponded with plots at Outer Island that were some 1 to 2 m deeper. This means that the same species from Billie Rocks do occur at Outer Island but at slightly greater depths. The

Table 2.4. Summary of two-way species sample matrix, obtained with TWINSPAN. Each column represents one or more partions of samples into clusters. Matrix values (1-8), are medians of ranks for biomass values (g DW quadrat^{-1}) of species in clusters (n = 5). Environmental variables for each sample cluster are given at the top of the table (for scaling see materials and methods), BR = Billie Rocks, OI = Outer Island.

Cluster	A		B				C			D				E
First division	0	0	0	0	0	0	0	0	0	0	0	0	0	1
Second division	0	0	0	0	0	0	0	0	0	1	1	1	1	
Third division	0	0	0	0	0	0	1	1	1					
Fourth division	1	1	0	0	0	0								
Site	OI	OI	OI	OI	OI	OI	BR	BR	BR	OI	OI	OI	BR	OI
Depth	14	17	20	23	26	29	5	8	11	5	8	11	2	2
Substrate	4	1	1	5	6	6	3	3	6	1	2	2	1	1
Slope	40	10	10	40	20	10	70	45	15	40	30	60	45	60
Callophyllis sp								1						
Ascoseira mirabilis							5	4						
Picconiella plumosa		2		1			2	1	1					
Hymenocladiopsis crustigena			2				1	1	1					
Delesseria lancifolia	1	1	1	1			2	1	1					
Georgiella confluens	1			1	1				2					
Hymenena laciniata		1												
Himantothallus grandifolius	4	4	5	5	4		4	4	7		3	4	1	
Pantoneura plocamioides	1	2	2	2	1		2	4	4	2		2		
Myriogramme mangini	2	1	1	1	1		4	4	4	3	4	2	3	
Kallymenia antarctica	2	3		1			2			2	1	2	1	
Phyllophora appendiculata		2	2			1	4	4	2		2		4	
Plocamium cartilagineum	5	5	4	4	4	4	4	4	2	2	2	4	4	
Delisea pulchra	1		3	1			1					2		
Delesseria sp	1	2	1						1	1	1			
Sarcodia montagneana				1	1			1					1	
Desmarestia anceps	3	5					4	6		6	4	8		
Gigartina skottsbergii							2			4			2	
Phycodrys antarctica							1	1	1	2	2		1	
Curdiea racovitzae				2									4	
Indaea cordata								2	2	2	1		4	4
Desmarestia menziesii										7	6	7	7	
Delesseria salicifolia											1			
Adenocystis utricularis														1
number of Phaeophyta	2	2	1	1	1	0	3	3	1	2	3	3	2	1
number of Rhodophyta	8	9	8	10	4	3	11	11	11	8	8	5	9	1
total species number	10	11	9	11	5	3	14	14	12	10	11	8	11	2

ordination diagram shows that no species have their optimum at depths greater than 20 m. Examples of species mainly occurring between 10 and 20 m are *Plocamium cartilagineum*, *Hymenocladiopsis crustigena*, *Delisea pulchra*, *Sarcodia montagneana*, *Georgiella confluens* and *Himantothallus grandifolius*. Examples of species with their centre of distribution at shallow depths are *Adenocystis utricularis*, *Curdiea racovitzae*, *Iridaea cordata* and *Gigartina skottsbergii* (Fig. 2.4). Species mainly occurring where the substratum consists of small boulders and pebbles include *Himantothallus grandifolius* and *Pantoneura plocamioides*.

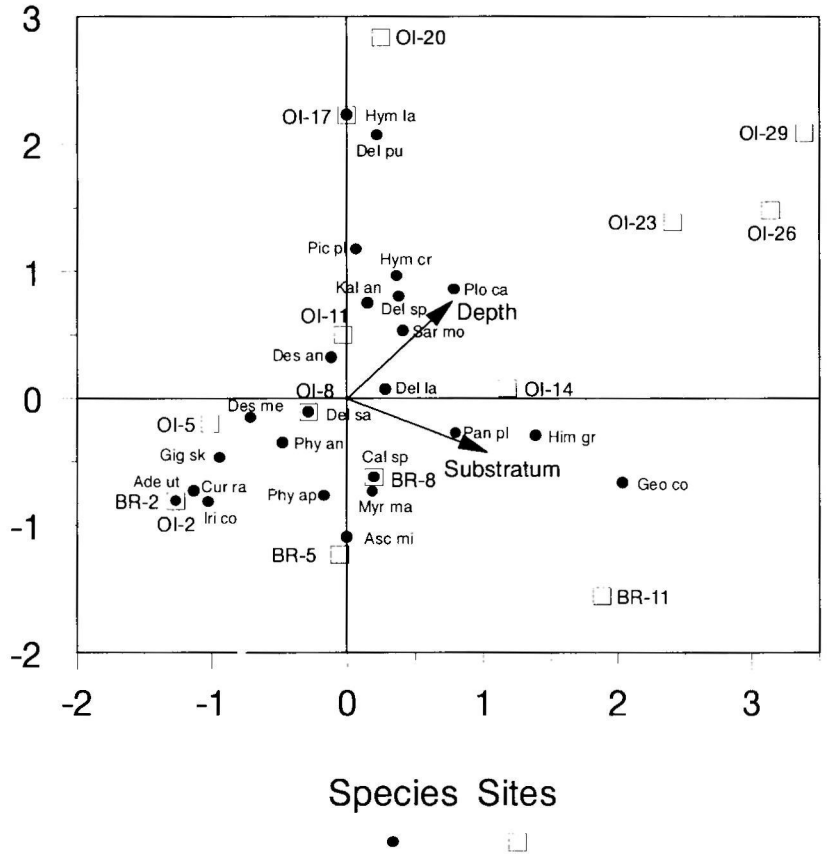

Figure 2.4. Results of canonical correspondence analysis of Billie Rocks and Outer Island (n = 5), using 2 environmental variables (substratum and depth). Biplot showing the position of species (●), the plots (□), and the environmental variables (arrows) on the first (horizontal) and second (vertical) ordination axis. Eigenvalues of axes 1 and 2 are 0.61 and 0.15 respectively. Percentage variance of species data explained by axis 1 is 25% and by axes 1 + 2 is 32%. Percentage variance of species-environment relation accounted for by axis 1 is 80% and by axes 1 + 2 is 100%. Labels for species and sites as in Table 2.2. BR-2 = Billie Rocks 2 m depth; OI-5 = Outer Island 5 m depth; etc

Modelling

For each species an attempt was made to relate presence-absence scores to water depth for the two sites, based on biomass or percentage cover data in the quadrats. The significant sigmoid and Gaussian response curves ($p<0.05$) are shown in Fig. 2.5. The values for the constant b_0 and coefficient b_1 and b_2 of these response functions are given in Table 2.5. The total percentage of correctly predicted presence-absence data with the models varied between 66 and 90% (Table 2.5).

Table 2.5. Constant (b_0) and coefficients (b_1, b_2) of the equations of the significant models are shown, together with the calculated optimum (u) and 95% reliability range (u_{lower} and u_{upper}), tolerance (t) and the maximum probability of occurrence (p_{max}) of the Gaussian response curves. Minima are marked with *. % corr. pred. = the total percentage of correct predicted presence-absence data (and percentage of correct predicted presence data). BR = Billie Rocks, OI = Outer Island, abbreviations as in Table 2.2.

Site	Species	b_0	b_1	b_2	u	u_{lower}	u_{upper}	t	p_{max}	% corr. pred.
% cover data										
BR	Des. an.	-11.35	3.88	-0.26	7.5			1.39	0.96	84 (81)
BR	Him. gr.	-6.80	0.86							82 (89)
BR	tot. red.	6.77	-1.80	0.11	8.2*				0.35*	67 (85)
OI	Des. an.	-2.33	0.51	-0.02	12.8	11.6	14.7	5.00	0.72	64 (53)
OI	Him. gr.	-6.32	0.76	-0.02	19.0	17.5	23.7	5.00	0.71	78 (77)
OI	tot. red.	2.37	-0.47	0.02	11.8*	6.8	20.1		0.40*	66 (90)
Biomass data										
BR	Myr. ma.	-1.98	0.74							85 (88)
BR	Pan. pl.	-4.13	0.78							80 (75)
OI	Iri. co.	2.51	-0.55							90 (57)
OI	Pan. pl.	-3.14	0.14							75 (30)
OI	Plo. ca.	-1.86	0.24							73 (85)

Presence-absence scores based on the percentage cover data resulted in models for *Desmarestia anceps*, *Himantothallus grandifolius* and Rhodophyta at Billie Rocks as well as Outer Island (Fig. 2.5, *top*). Although the resulting pattern is rather similar, the probabilities of occurrence are higher at Billie Rocks at comparable depths. Furthermore, both *Desmarestia anceps* and *Himantothallus grandifolius* reach their optimum at greater depths at the exposed site Outer Island. *Himantothallus grandifolius* and *Desmarestia anceps* can occur about 5 m higher in the sublittoral of the sheltered site Billie Rocks compared with the exposed site Outer Island. The calculated maximum probability of occurrence (p_{max}) for *Desmarestia anceps* is 0.96 at Billie Rocks and 0.72 at Outer Island and the optimum (u) is at 7.5

m and 12.8 m, respectively (Table 2.5). The p_{max} for *Himantothallus grandifolius* was 0.71 at Outer Island and the predicted optimum was laying at 19 m. Reliability intervals of the optima are given where possible, but could not be calculated for the cover data at Billie Rocks. At both sites the Rhodophyta show a minimum in probability of occurrence and the minimum at Outer Island is achieved at greater depth.

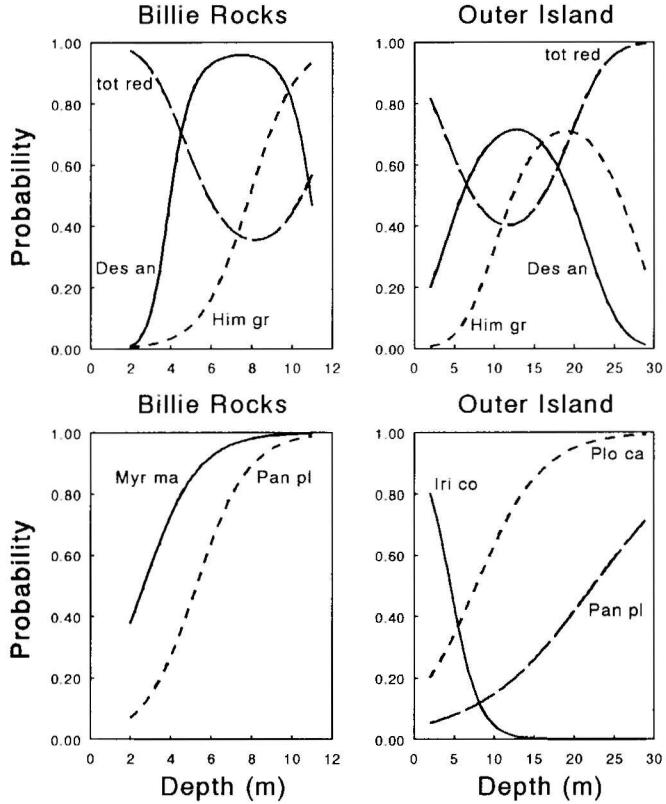

Figure 2.5. Significant models ($p<0.05$) showing the probability of occurrence for *Himantothallus grandifolius*, *Desmarestia anceps* and Rhodophyta based on percentage cover data (*top*), and *Iridaea cordata*, *Plocamium cartilagineum* and *Pantoneura plocamioides* based on biomass data (*bottom*) as a function of depth at Outer Island and Billie Rocks. Abbreviations are shown in Table 2.2

For single species of Rhodophyta only standing crop (g DW m^{-2}) but no cover data were available. Significant models ($p<0.05$) were obtained for *Pantoneura plocamioides* and *Myriogramme mangini* at Billie Rocks and *Iridaea cordata*, *Plocamium cartilagineum* and *Pantoneura plocamioides* at Outer Island (Fig. 2.5, *bottom*). These models showed an increase in probability of occurrence with increasing water depth, except for *Iridaea cordata* at Outer Island for which

probability decreased with increasing depth In this data set, based on standing crop, none of the Rhodophyta fits a Gaussian response curve. From the standing crop data no significant response curves could be obtained for the Phaeophyta.

Although for Signy Island no biomass or percentage cover data are available from depths exceeding 29 m, incidental deeper observations showed *Plocamium cartilagineum* These occasional observations to a depth of 38 m did show a sparser density of Rhodophyta and an increasing number of faunal taxa such as Bryozoa, Porifera and Anthozoa.

Zonation pattern

From the results as shown in the Figs 2 1-2 3 and 2.5 the vertical distribution of the sublittoral macroalgal vegetation of Signy Island can be divided in an ice-abraded zone with mainly *Iridaea cordata*, a zone 5 to 14 m dominated by *Desmarestia anceps* and *Desmarestia menziesii* and a zone 15 to 25 m depth dominated by *Himantothallus grandifolius* Below 25 m *Plocamium cartilagineum* is dominant

Discussion

Of the 36 species recorded in this study, 15 species, mainly belonging to Rhodophyta, had not been previously recorded for Signy Island This shows the importance of detailed and up-to-date studies on macroalgal floras in Antarctic waters, as older studies might be incomplete. The overall species list shows strong similarities to those reported from locations on the Antarctic Peninsula (Amsler et al. 1990, Chung et al 1990, 1994, DeLaca and Lipps 1976, Delépine et al. 1966, Kloser et al. 1994, Lamb and Zimmerman 1977, Moe and DeLaca 1976, Neushul 1965, Zielinski 1990). In high Antarctic regions Phaeophyta of large size are lacking and species numbers are smaller than at Signy Island (Cormaci et al. 1992, Miller and Pearse 1991), while at sub-Antarctic islands much higher numbers are recorded (John et al. 1994, Ricker 1987) There seems to be a decrease in species diversity and an increase in endemism of Antarctic macroalgae with increasing latitudes (Heywood and Whitaker 1984), which contrasts with the Arctic benthic algae, as their diversity and their degree of endemism both decrease with higher latitudes (Lee 1973) According to Dayton (1990) the differences in north and south polar benthos are due to differences in origin and evolution, oceanic habitats and climates and the type of terrestrial influence.

Patchiness in the distribution pattern of Antarctic macroalgae causes within-site variation in the biomass data of the macroalgae with depth and exposure and requires detailed data for comparison Combining a photographic method with a harvesting method gave more complete information about the zonation of sublittoral

macroalgae at Signy Island than any of these methods on its own would have done. While the photographic method proved inadequate to establish the abundance of the species in the understory of the vegetation and to identify the Rhodophyta to species level, this information was obtained from the standing crop data The photographic method on the other hand showed a more realistic view of the upper canopy of the vegetation. Macroalgae attached in a quadrat were not standing upright in the water column like kelp communities, but were laying flat on the substratum. The quadrat size might have been too small for the Phaeophyta and too large for the Rhodophyta, but the size was a compromise between trying to collect as much information as possible in physically exacting and sometimes hazardous circumstances, working safely at the same time and influencing the environment as little as possible.

The maximum biomass found at Outer Island (8 8 kg WW m^2) was more than four times the maximum biomass of 2.1 kg WW m^2 found by Richardson (1979) in Borge Bay, at a transect perpendicular to Billie Rocks in northern direction with maximum depth of 13 m Compared with the sub-Antarctic vegetation the biomass of Signy Island macroalgal vegetation is relatively low No other standing crop data of macroalgal vegetation are available from further south. Biomass values in the literature for Phaeophyta in sub-Antarctic waters have a mean of 11.6 kg WW m^2 for *Macrocystis laevis* at the Prince Edward Islands (Attwood et al 1991), a range of 3.4-22.5 kg WW m^2 for *Macrocystis pyrifera* at the Kerguelen (Delépine 1976), and an extreme maximum of 226.0 kg WW m^2 for *Durvillaea antarctica* at Kerguelen (Lawrence 1986) The high standing crop value for *Durvillaea antarctica* is probably caused by taking the quadrat in the narrow fringe along the lower intertidal zone where *Durvillaea antarctica* is growing and not taking into account the patchiness in the distribution pattern (Lawrence 1986). As shown above, regional differences do exist. They make comparison of sites difficult and make it very difficult to distinguish, for example, latitudinal trends.

The zonation pattern found in this study for Signy Island is similar to zonation patterns found at Anvers Island and King George Island (Amsler et al. 1990, Chung et al. 1994), although the characteristic species and the lower distribution limits of the species were different. At King George Island, *Palmaria decipiens* (Rhodophyta) dominated the first 5 m, *Desmarestia menziesii* and *Ascoseira mirabilis* the zone of 5-15 m, and *Himantothallus grandifolius* below 15 m (Chung et al. 1994). At Anvers Island, Amsler et al. (1990) found *Desmarestia anceps* and/or *Desmarestia menziesii* dominant at depths shallower than 5 m *Desmarestia antarctica* dominated at 10-15 m and *Himantothallus grandifolius* represented the zone below. On the coast of the Weddell Sea and the Ross Sea, the species composition of algal communities is very different, with *Phyllophora antarctica* being the dominant species in the lower infralittoral and upper sublittoral (Cormaci et al. 1992, Kirkwood and Burton 1988,

Miller and Pearse 1991).

Diversity and abundance of macroalgae depend on many environmental, chemical and biological factors. In Antarctic waters, the low species number and low biomass may be related to adverse physical conditions such as low water temperatures, reduced light caused by ice cover and seasonal solar declination, and ice scour. The most abundant and diverse aggregations of benthic flora seem to be in open areas exposed to waves and currents (Moe and DeLaca 1976, Zielinski 1990). Our observations of macroalgal diversity and biomass at Billie Rocks compared with Outer Island at the same depths, suggest that this may be so for the brown macroalgae (Fig. 2.1). The biomass of Rhodophyta, however, is higher for comparable depths at the sheltered site (Fig. 2.2).

Moe and DeLaca (1976) suggested that differences in algal assemblages in the Antarctic region are caused by a difference in light penetration (inshore turbid water or offshore clear water). These differences may be related, for example, to suspended sediments in the water column, shading by the phytoplankton bloom, temperature differences in the water column, duration of ice cover, ice quality and ice thickness (Klöser et al. 1993). During winter, few differences exist in the time of arrival of sea ice between Outer Island and Billie Rocks, as the arrival of pack ice in Borge Bay is usually the factor which allows the surface of Factory Cove to freeze (Clarke et al. 1988). This process does create several metres of thick pack ice at Outer Island and relatively thinner sea ice at Billie Rocks, which could well be an advantage for inshore macroalgae as their growing season starts in spring and early summer (Dieckmann et al. 1985, Drew and Hastings 1992, Hastings 1977, Wiencke 1990a, 1990b). Light measurements carried out in Borge Bay showed a strong decrease of light penetration when sea ice cover is present (Gilbert 1991). These small differences in ice conditions do not explain the more abundant brown macroalgal vegetation at Outer Island, as the thick ice cover causing low light intensities contrasts with the overall high biomass of macroalgae, but the differences could play a role in creating more favourable light circumstances for macroalgae to grow higher in the sublittoral of Billie Rocks.

Another influence of a thick layer of ice is scouring, which causes more damage at Outer Island and over a greater depth. The higher biomass of red macroalgae at the shallow depths of Billie Rocks is possibly related to the less intense ice-scouring. An explanation for the abundant vegetation of Outer Island probably still has to be found in factors which play a more important role in the summer period, such as waves and currents causing more turbulence in the water column and phytoplankton blooms present at Signy from December till February (Clarke et al. 1988). Biological interactions, such as competition for space and light, may be more important in spring and early summer. The explanation for the shift towards abundant and deeper macroalgal vegetation at Outer Island might be found in a combination of biological

factors and level of exposure in the summer period.

The greatest depth where *Himantothallus grandifolius* still can be expected seems to be around 35 m (Fig. 2.5). But, as the depth range studied in this paper lies between 2 and 29 m, little can be said about shallower and greater depths. Wiencke (1990a, 1990b) predicted lower distribution limits of *Adenocystis utricularis*, *Ascoseira mirabilis*, *Acrosiphonia arcta*, *Palmaria decipiens*, *Enteromorpha bulbosa*, *Iridaea cordata* and *Gigartina skottsbergii*, based on minimum light requirements in long-term culture studies. These limits were 28 ± 5 m (20 ± 4 m for *Iridaea cordata* and *Gigartina skottsbergii*) for inshore areas with little exchange with the ocean, and 53 ± 23 m for offshore waters. Klöser et al. (1993) concluded that, with the conditions for light penetration in Potter Cove, King George Island, a limit of 0.2% of surface irradiance for macroalgal growth resulted in a depth limit of 40 m. The reports of extremely deep (hundreds of metres) occurring Antarctic flora (Zaneveld 1966) are therefore probably the result of transportation of detached algae to greater depths, and not growth *in situ*.

Using models in this study was a first attempt to relate occurrence of macroalgae to environmental factors. It appeared to be impossible to obtain a response curve for each separate species, probably because of a relatively small number of observations. The models are based on the situation at Billie Rocks and Outer Island and therefore models from other sites and greater depths might well be different. Combining results from other studies on sublittoral macroalgal zonation carried out on different locations in the Antarctic might lead to a generalized model with a predicting value.

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Photosynthetic performance *in situ* of the brown macroalga *Desmarestia anceps* Montagne from Signy Island (Antarctica)

Patty EM Brouwer

Abstract

The photosynthetic characteristics of one of the dominant brown macroalgae at Signy Island (South Orkney Islands, Antarctica), *Desmarestia anceps* Montagne, were studied in different periods of the year under natural irradiance levels by use of specially developed incubation chambers. The results demonstrate that *Desmarestia anceps* is well adapted to low irradiance levels. The initial saturation irradiance (I_k) varied, not significantly, from 14.6 ± 1 9 µmol m^{-2} s^{-1} in spring to 23.0 ± 3.3 µmol m^{-2} s^{-1} in summer Mean gross photosynthetic capacity ($P_{g\ max}$) showed seasonality, and was significantly higher in spring with 61 3 ± 3.7 µmol O_2 g^{-1}DW h^{-1} than in winter with 49.6 ± 1 2 µmol O_2 g^{-1}DW h^{-1} The photosynthetic efficiencies (α) were high in all seasons and reached in spring an α value of 4 2 ± 0.3 µmol O_2 g^{-1}DW h^{-1} (µmol m^{-2} s^{-1})$^{-1}$, which was significantly higher than in summer and winter. Compensation irradiance (I_c) was low and showed a very limited range from 1 0 to 1 3 µmol m^{-2} s^{-1}. Chlorophyll *a* content was different between all seasons, but more information on the total pigment content is required for correlations with $P_{g\ max}$ or α. Estimates of annual net production rates were 163 8 and 10.7 mmol O_2 g^{-1}DW y^{-1} at 5 and 25 m depth, respectively The data predict a maximum depth of occurrence at 27.7 m. Irradiance levels to a depth of 25 m were not limiting the occurrence of *Desmarestia anceps*, but did reduce maximum oxygen production rates.

Introduction

Information available on Antarctic macroalgae has for a long time been limited to taxonomical and biogeographycal studies (reviewed in Heywood and Whitaker 1984, updated by Brouwer et al 1995, Chung et al. 1994, Cormaci et al. 1992, Dayton 1990, Kloser et al 1994, Moe and Silva 1989). More recently studies on photosynthetic responses of macroalgae were carried out under laboratory conditions (Post and Larkum 1993, reviewed by Wiencke 1996). From these laboratory studies Antarctic macroalgae are characterized as being shade adapted, and used to a high variation in irradiance and seasonal changes of daylength as well as to low water temperatures (reviewed by Kirst and Wiencke 1995). Field measurements of growth and productivity of Antarctic macroalgae are generally lacking, while in non-polar areas field studies have been carried out more frequently (e.g. references in Davison 1991, Henley 1993, Huppertz et al. 1990). One of the problems of studying sublittoral macroalgae *in situ* is that SCUBA equipment or even submersibles are required (e.g. Shepherd and Womersley 1970, Littler et al. 1985), and in polar waters supplementary difficulties for using SCUBA equipment are present (e.g. cold, freezing of equipment) In the Arctic, particularly one endemic species, *Laminaria solidungula*, has been studied intensively (Chapman and Lindley 1980, Dunton 1985, 1990, Dunton and Jodwalis 1988, Dunton and Schell 1986, Dunton et al. 1982, Henley and Dunton 1995). This species grows hardest in winter and early spring under thick ice cover when nutrients are available for new tissue growth and light conditions not being optimal (Chapman and Lindley 1980, Dunton et al. 1982).

Compared to macroalgae from non-polar regions, polar macroalgae not only have to deal with extreme seasonal changes of daylength and changes in the light climate caused by wave action and storms (Lobban and Harrison 1994), but also have to face reduced irradiance levels caused by ice cover in winter. As water temperature and salinity are relatively constant, and nutrient levels are high in Antarctic waters (Clarke et al. 1988), the most important factor affecting the seasonal growth of macroalgae must be light. Arctic species have to deal with similar environmental conditions as Antarctic species. Unfortunately, few photosynthetic studies have been carried out on Arctic macroalgae in contrast to a large number of studies on ice algae and phytoplankton (reviewed by Kirst and Wiencke 1995). *Laminaria solidungula* is an exception and has been studied for the photosynthetic characteristics (Dunton and Jodwalis 1988).

The only *in situ* study of primary production carried out at an Antarctic macroalgal species has been performed on the brown kelp-like macroalga *Himantothallus grandifolius* Skottsberg (Drew and Hastings 1992). Maximum photosynthetic rates were found for this species in November and respiration rates were higher than production rates at the end of March Data about seasonal photosynthetic performance of algae collected in the field are available for *Adenocystis utricularis* (Bory) Skottsberg

(Gutkowski and Maleszewski 1989) and *Ascoseira mirabilis* Skottsberg (Gómez et al. 1995) *Adenocystis utricularis* showed an increased photosynthetic capacity in the winter months. Similarly, in *Ascoseira mirabilis* maximum photosynthetic rates were higher in September compared to October-February.

For extending our knowledge of Antarctic macroalgal photosynthesis under field conditions the photosynthetic characteristics of *Desmarestia anceps* Montagne were determined in different seasons *in situ* and annual production rates were predicted at different depths. *Desmarestia anceps* was chosen in this study, as it is one of the dominant species in the macroalgal vegetation of Signy Island (Brouwer et al. 1995).

Materials and methods

Study area and macroalgal material

The present study was carried out in February (summer), July-August (winter), and September-October (spring) 1993 at three different sites in Borge Bay, Signy Island, Antarctica (60°42'S, 45°36'W; Fig. 1.1). Adverse weather conditions (windspeed > 23 knots) often limited the diving and boating range to the inner site of Borge Bay, where Factory Cove and Billie Rocks were used for the 0.5 m and 5 m depth measurements, respectively. The seawater sampling site (SW) in Borge Bay was used for the 25 m depth measurements in good weather conditions (windspeed ≤ 23 knots). In summer at Signy Island, daylength reaches a maximum of 19 h and in winter a minimum of 6 h. During the winter, sea-ice is present for an average of 135 days each year, with a large year to year variation (Murphy et al. 1995), which limits light penetration to greater depths. Seawater temperature shows a small seasonal variation, from -1.8°C in winter to +0.3°C in summer, while salinity is constant (33.9 ‰ ± 0.5) apart from occasional slightly lower surface values caused by melt water (Clarke et al. 1988). Nutrient levels in the water are high during the whole year, with minimum levels for nitrate, nitrite and phosphate in summer during phytoplankton blooms, and minimum levels for ammonia in late winter (Clarke et al. 1988).

Macroalgae are abundant on the rocky coast of Signy Island and *Desmarestia anceps* Montagne (Desmarestiales), one of the dominant species from the total of 36 species found at Signy Island, occurred at a range from 2 to 30 m depth below mean low water (MLW) (Brouwer et al. 1995). Macroalgal fronds (varying between 13.6 and 97.8 g wet weight and a length of approximately 30 cm) were sampled by SCUBA diving at Billie Rocks, Bare Rock or Outer Island and either directly used in the experiment or after transport in an insulated box to the laboratory, kept, for at most two days in the laboratory with a continuous flow of seawater pumped directly from Factory Cove Fronds were always collected from the peripheral ends of the bushy adult plants, causing one wound (≤ 0.5 cm) on the main branch. Table 3.1 summarizes the incubation

dates, sites and depths, sampling sites and depths, and ranges of dry weights and chlorophyll *a* contents of *Desmarestia anceps* fronds used in the incubations.

Table 3.1. Incubation sites and depths (m), sampling sites and depths (m), ranges of dry weights (DW as % of wet weight) and chlorophyll *a* content (Chl *a* in mg Chl *a* g^{-1}DW) of the *Desmarestia anceps* fronds used for the measurements SW = seawater sampling site, FC = Factory Cove, BR = Billie Rocks, BaR = Bare Rock, OI = Outer Island, fr is number of fronds used

Season	Incubation site	Incubation depth	Sampling site	Sampling depth	fr	DW range	Chl *a* range
Summer[1]	SW	0 5	BaR, BR	7, 8	4	15 5-18 6	1 7-2 2
	SW	5	BR, OI	6, 22	8	15 3-23 2	1 6-2 0
	SW	25	BaR, OI, BR	6, 22	6	17 3-20 6	1 6-2 2
Winter[2]	BR, FC	0 5	BR, OI	5-8, 15	11	17 2-19 9	0 8-1 7
Spring[3]	BR	5	BR	5 6	4	14 7-16 9	2 0-2 7

[1] incubation dates 3, 11, 15, 16, 17, 18, 20, 23, 24 and 25 February 1993
[2] incubation dates 23, 27 and 28 July and 2, 4 and 10 August 1993
[3] incubation dates 30 September and 6 October 1993

Oxygen evolution measurements in situ

Photosynthetic incubations of the *Desmarestia anceps* fronds were conducted *in situ* by placing two cylindrical self-registering plexiglass incubation chambers at equal depth A custom-made incubation chamber consisted of two compartments, had a total height of 57 cm and a diameter of 30 cm The closed upper compartment was sealed with an O-ring, had a volume of 13 litre, was equipped with a 2π PAR (photosynthetical active radiation) light sensor (BPW 21, Skiltronics BV, Leeuwarden), two YSI 5739 oxygen electrodes with temperature sensors (Yellow Springs Instruments Inc , Ohio) and a custom-made stirring mechanism One of the electrodes was used in the calculations, the second one was used as back up The stirrer was fixed at equal distance between the two electrodes in a flow-through channel, sucking water from the middle and pushing water towards the sides of the chamber A continuous flow of water over the electrodes resulted in a stable signal of the electrodes The oxygen consumption of the electrodes was negligible Mixing of the water in the upper compartment, tested with ink, was rapid and consistent The cosine-corrected light sensor was attached to the roof of the upper compartment, so that downwelling irradiance was measured The open lower compartment contained a data logger (Seawise, Den Helder) in a pressure free, water tight tube, and the underwater cables connected the light sensor, electrodes and stirrer of the upper compartment with the data logger Oxygen concentration, water

temperature and irradiance (PAR) were recorded every 90 seconds by the data logger on a scale from 0 to 998 units (with an accuracy of 0.1%) In periods free of sea-ice, the incubation chambers were positioned in the water at a depth of 0.5, 5 or 25 m with stainless-steel cables, connected to durapipe rafts of 1 m x 1 m, which were floating on the surface, and anchored separately to the bottom. In periods when sea-ice was present the incubation chambers were attached directly, with stainless-steel cables, from an anchorage on the ice surface.

Winkler titrations (Grasshoff et al. 1983) to calibrate the oxygen electrodes were carried out ten times during the study, including the times when membranes were changed, with seawater from Factory Cove under the same temperatures as in the field. The oxygen evolution was expressed in mg O_2 l^{-1} h^{-1} by linear regression between the change in oxygen concentration over time For the two incubation chambers, the mean coefficients of the regression lines (y = ax + b) were 40.0 ± 3 7 and 35.7 ± 6.2, respectively, and the mean constants were -30 9 ± 12 1 and -23.6 ± 10 2, respectively (r^2 >0.99, n = 11-22). The light sensor of the incubation chamber was cross-correlated in the laboratory with a Li-cor quantum meter (LI-185B, Li-cor Inc) and a Li-cor sensor (LI-192SB, Li-cor inc) Results were averaged over one hour and given in µmol m^{-2} s^{-1}. After each measurement the macroalgal material was blotted with tissue paper to determine wet weight (WW). The variation in WW using the blotting method was 7.8%. Sub-samples were dried at 60-80°C for at least 48 hours to obtain dry weight (DW). Photosynthetic rates were expressed in units of µmol O_2 g^{-1}DW h^{-1} Part of the fresh material was frozen at -40°C for chlorophyll *a* analysis. Chlorophyll *a* was measured by freeze-drying the plant material, grinding it using a ball-mill and extracting it with 90% acetone for 24 h The amount of chlorophyll *a* was determined by high-performance liquid chromatography (Millipore Waters) according to the method of Brown et al (1981).

Measurements on the uptake and release of oxygen by the *Desmarestia anceps* fronds in relation to the irradiance were made for periods varying from several hours to a maximum of 24 hours Weather conditions, such as strong winds, incoming ice bergs or drifting pack ice often shortened the length of incubation times At first incubations were carried out as long as possible for gathering as much information and to measure respiration during natural periods of darkness Later it was decided, only to use the first 2 to 3 hours of incubation in this study, as a maximum of 32% supersaturation occurred in summer, and increasing oxygen concentrations during incubations inhibit photosynthesis (Gordon and Sand-Jensen 1990) As respiration rates were only determined during the night it was assumed that this rate was the same as the respiration during the day-light period, although in literature, there are indications of lower respiration levels in the light (Kelly 1989, Noggle and Fritz 1983, Raven and Beardall 1981) Incubation chambers containing only seawater were used as blanks and incubated regularly to determine the oxygen production/respiration of phytoplankton present in the seawater. Results were corrected for the blank measurements Seasonal production was estimated by plotting

the oxygen evolution in the incubation chambers as a function of irradiance (P-I curves) by non-linear curve fitting Data were fitted to different functions, and a Chi-Square goodness of fit test ($p<0.05$) was performed on each function As no photoinhibition was observed, the model of Platt and Jassby (1976) gave the best results

$$P_g(I) = P_{g\,max} \tanh (\alpha\, I / P_{g\,max}),$$

where $P_g(I)$ is the gross oxygen production in µmol O_2 g^{-1}DW h^{-1} and I is the underwater irradiance in µmol m^{-2} s^{-1} The programme used was PrimProd, version 2 1 (de Hoop 1994), giving mean values with SD in one curve of the light-saturated rate of gross photosynthesis ($P_{g\,max}$), the photosynthetic efficiency (α), as the initial slope of the photosynthesis versus irradiance curve in µmol O_2 g^{-1}DW h^{-1} (µmol m^{-2} s^{-1})$^{-1}$ and the initial saturating irradiance level ($I_k = P_{g\,max} / \alpha$) Gross production was estimated by adding the mean measured respiration (R) to the measured net oxygen production (P_n) A rough indication for the irradiance compensation point (I_c) was obtained by plotting the modelled gross oxygen production minus the respiration

Irradiance measurements

Irradiance at the surface was monitored by the British Antarctic Survey (BAS, unpublished data) using a CM 11-Pyranometer (spectral range 305-2800 nm, Kipp and Zonen, Delft) These readings were cross-correlated with the Li-cor quantum meter (spectral range 400-700 nm) by linear regression ($y = 1\,59x + 1\,63$, $r^2 = 0\,98$, $n = 31$) Throughout the year 17 incidental irradiance measurements were carried out at the seawater sampling site, with the Li-cor quantum meter, to determine the surface irradiance, the percentage of surface irradiance available just underneath the water or ice surface and at 5 to 25 m depth, with 5 m depth intervals The sensor was mounted on a 1 5 m long arm and lowered down to the depth desired, avoiding shading effects of the boat or people standing on the ice surface Thickness of sea ice and the layer of snow covering the ice were also measured by the British Antarctic Survey Details on the fluctuating irradiance levels at the different depths in the water column are given in Brouwer (1996) The daily surface irradiance in combination with the incidental irradiance measurements and the variation in ice present on the water surface were used to predict irradiance levels at the different water depths These predicted irradiance levels were used to model the annual production rates of *Desmarestia anceps*

Daily and annual production

Daily net production was calculated from the estimated daily irradiance levels at depth, based on the daily surface irradiance and incidental irradiance measurements, and the fitted net production, based on the P-I curves Predictions of annual net oxygen production were made by multiplying the modelled daily net production with the number

of days per month and adding these monthly data together Production measurements carried out in February, July-August and September-October were used for the summer, winter and spring P-I curves, respectively The seasons were in this study roughly defined by hours of daylength As autumn measurements were missing, summer period in this study lasted from November till April, winter period from May till August and spring from September till October.

Data analysis

Differences between photosynthetic characteristics of fronds sampled at different depths and incubated at the same depth were determined with a t-test. One way ANOVA compared the mean photosynthetic characteristics given by the model, the respiration rate and the chlorophyll *a* content for the seasons For differences between the seasons a Tukey-Kramer multiple comparison test was used. Differences were considered to be significant when the $p<0\ 05$

Results

Irradiance measurements

Details on the results of the irradiance levels are published in Brouwer (1996), and therefore only the main results are given here In summer, surface irradiance levels were high, caused by the sun relatively high on the horizon and long daylengths, while in the water column irradiance levels are reduced as a result of a dense phytoplankton bloom starting in December and lasting till February, and as a result of turbidity, caused by silt being in suspension due to storms The water column in winter, on the other hand, was very clear, because of an absence of phytoplankton blooms and with ice being present around the island, storms having less effect on silt in suspension. In winter surface irradiance levels are low, caused by the sun relatively low on the horizon and short daylengths In spring the presence of ice reduced the irradiance levels under water, while the water column was very clear Increasing daylengths in spring caused higher irradiance levels under water Irradiance levels measured in this study showed low values in general, and therefore photoinhibition under natural irradiance levels is not likely to occur The total annual irradiance received on the surface (4 42 kmol m^{-2}) decreased from 0 80 at 5 m depth to 0 05 kmol m^{-2} at 25 m depth (Table 3 4). Based on the incidental irradiance depth profiles, the extinction coefficient (k_d) integrated over the year was 0 158 m^{-1} Extrapolation of a linear regression between the annual net production and the logarithm of the annual irradiance ($P = 48\ 9\ \ln(I) + 161\ 5$, $r^2 = 0\ 98$, $n = 6$), would give a zero annual net production rate for *Desmarestia anceps* at 27 7 m depth (corresponding to 0 8% of surface irradiance)

Photosynthetic characteristics

In order to pool the results of fronds collected from different depths for one season, it was important to determine whether there were significant differences between the results of incubation at the same depth This was carried out for the summer season, and results are shown in Table 3.2. No significant differences were found for $P_{g\,max}$, α and I_k ($p>0.05$) Although it is concluded from phytoplankton and diatom studies that algae shifted from low to high irradiance levels decrease their pigments (Falkowski and LaRoche 1991), no evidence was found for this in *Desmarestia anceps*. Also Weykam (1996) found no significant differences in $P_{g\,max}$, I_k, α and chlorophyll *a* content in a laboratory experiment with *Desmarestia anceps* fronds collected freshly at 10, 20, and 30 m depth. No indications of similar photosynthetic characteristics of temperate macroalgae from different depths are found in literature, but similar pigment concentrations were found in a laboratory experiment, where the effect of shading up to 12.5% of day-light was studied on *Ascophyllum nodosum* (Cousens 1982). However, a possible explanation for the non-significancy between the photosynthetic characteristics might be the variation between the fronds used, giving a reflection of the natural variation in the population. Although the evidence for comparable photosynthetic characteristics and similar chlorophyll *a* content in *Desmarestia anceps* fronds collected at different depths is limited to two studies (this study, Weykam 1996), it was assumed that data could be pooled per season

The seasonal P-I curves, showing the realtionship between the mean net oxygen production or respiration of *Desmarestia anceps* and the underwater irradiance, are shown in Fig. 3 1. Irradiance values measured in the field during these *in situ* incubations ranged from 0 to 202 µmol m^{-2} s^{-1}. In spring, *Desmarestia anceps* reached maximum production rates at lower light levels than in winter and summer. The seasonal variation in photosynthetic characteristics of the *Desmarestia anceps* fronds are summarized in Table 3.3. $P_{g\,max}$ in winter averaged 49.6 ± 1 2 µmol O_2 g^{-1}DW h^{-1} and was significantly

Table 3.2. Photosynthetic characteristics of *Desmarestia anceps* fronds sampled in summer at 6 m and 22 m depth, but both incubated at 5 m depth Units $P_{g\,max}$ (µmol O_2 g DW h^{-1}), α (µmol O_2 g^{-1} DW h^{-1} (µmol m^{-2} s^{-1})$^{-1}$), I_k (µmol m^{-2} s), total number of fronds used per incubation depth is 4, with P_g in duplicate at 9 irradiance levels, mean values with SD in brackets

Parameter	Sampled at 6 m depth[1]	Sampled at 22 m depth[2]	
$P_{g\,max}$	52 5 (1 9)	48 4 (2 8)	ns
α	2 6 (0 4)	2 2 (0 4)	ns
I_k	20 4 (3 5)	21 9 (5 0)	ns

[1] incubation dates 15 and 16 February 1993

[2] incubation dates 18 and 20 February 1993

ns = no significant differences between sampled at 6 m depth and 22 m depth ($p>0$ 05)

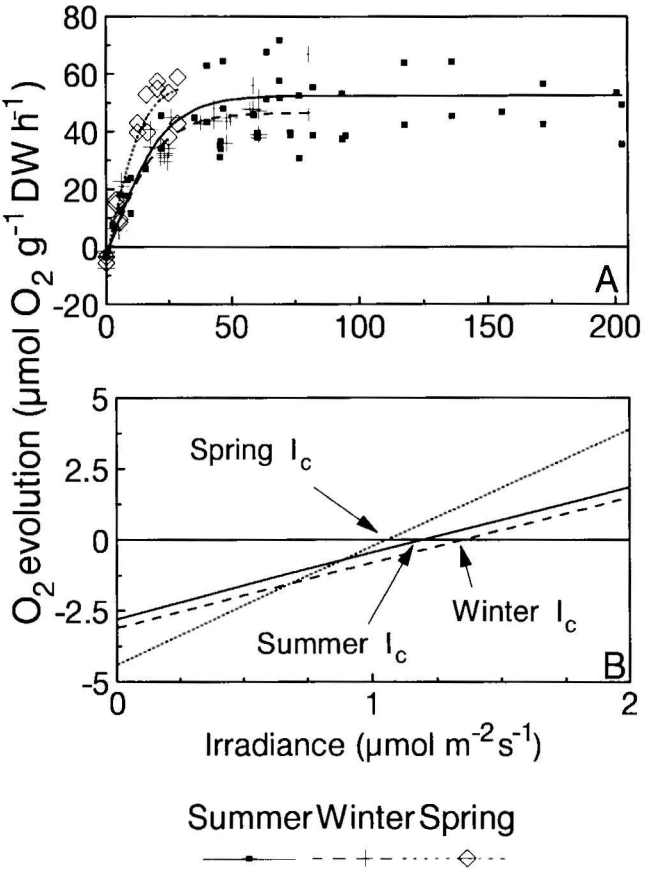

Figure 3.1. Relationship between net oxygen production rate, respiration rate (µmol O_2 g^{-1}DW h^{-1}) and the irradiance (µmol m^{-2} s^{-1}) with fitted P-I curves for summer, winter and spring measurements. Individual points show the original data pooled per season (A). Enlargement of the low irradiance levels shows the modelled irradiance compensation points (I_c) for winter, summer and spring (B)

lower than in spring ($p<0.05$), while rates in summer and spring were not significantly different ($p>0.05$) reaching a maximum in spring of 61.3 ± 3.7 µmol O_2 g^{-1}DW h^{-1}. No significant differences were found between summer and winter $P_{g\ max}$ ($p>0.05$). Photosynthetic efficiencies (α) were high in all seasons and reached a maximum of 4.2 ± 0.3 µmol O_2 g^{-1}DW h^{-1} (µmol m^{-2} s^{-1})$^{-1}$ in spring, which was significantly higher than in summer and winter ($p<0.05$). No significant difference in α was found between summer and winter ($p>0.05$). The initial saturating irradiance level (I_k) ranged between the seasons from 14.6 ± 1.9 in spring to 23.0 ± 3.3 µmol m^{-2} s^{-1} in summer, but the difference was not significant ($p>0.05$). Low irradiance compensation points were found, ranging from 1.0 to 1.3 µmol m^{-2} s^{-1} (Fig. 3.1 and Table 3.3). Respiration rates did not differ

significantly between the seasons ($p>0.05$). Chlorophyll *a* content was the lowest in winter with 1.2 ± 0.4 mg Chl *a* g^{-1}DW and highest in spring with 2.4 ± 0.4 mg Chl *a* g^{-1}DW and significantly different between all seasons ($p<0.05$). Table 3.3 also summarizes the photosynthetic characteristics of *Desmarestia anceps* tissue obtained from laboratory experiments with cultured and fresh material. Both Wiencke et al. (1993) and Weykam et al. (1996) found higher values for $P_{g\,max}$, $P_{n\,max}$, R, I_c and I_k. Only α values were comparable with results obtained from this study.

Table 3.3. Seasonal variation in photosynthetic characteristics of *Desmarestia anceps* fronds obtained from models based on data grouped per season with maximum irradiance level of 202 µmol m^2 s^{-1}. Units: $P_{g\,max}$, $P_{n\,max}$ and R (µmol O_2 g^{-1}DW h^{-1}); α (µmol O_2 g^{-1}DW h^{-1} (µmol m^2 $s^{-1})^{-1}$); I_c and I_k (µmol m^2 s^{-1}); Chl *a* as chlorophyll *a* content (mg Chl *a* g^{-1}DW); mean values with SD in brackets. For comparison, photosynthetic characteristics determined in previous laboratory studies are included

Parameter	This study summer[1]	This study winter[2]	This study spring[3]	Wiencke et al. (1993) cultures[4]	Weykam et al. (1996) fresh material[5]
$P_{g\,max}$	55.3 (1.7)	49.6 (1 2)	61.3 (3.7)	130.6	228.4
α	2.4 (0.3)	2.3 (0.1)	4.2 (0.3)	4.1 (1.4)	6.7 (1.6)
I_k	23.0 (3.3)	21.2 (1.6)	14.6 (1.9)	32.3 (1.8)	32.1 (3.1)
R	2.8 (0.9)	3.1 (1.6)	4.4 (0.9)	18.1 (3.8)	106.6 (19.4)
I_c	1.2	1.3	1.0	4.3 (0.7)	15.5 (1.1)
$P_{n\,max}$	52 5	46 5	56 9	112.5 (3.1)	121.8 (3.1)
Chl *a*	1 8 (0.2)	1.2 (0 4)	2.4 (0.4)	6.2 (0.1)	3.7 (0.2)

[1] total number of fronds used is 18, with P_g in duplicate at 30 irradiance levels; for R: n = 3
[2] total number of fronds used is 11, with P_g in duplicate at 21 irradiance levels, for R. n = 6
[3] total number of fronds used is 4, with P_g in duplicate at 12 irradiance levels, for R: n = 4
[4] Unialgal cultures of isolates from King George Island, grown under simulated Antarctic daylengths and 0°C in the laboratory, n = 4
[5] Fresh material sampled at King George Island from the end of October till start of December, and used in laboratory experiments, n = 3 or 4

Daily and annual production rates

A prediction, for different depths, of the daily net oxygen production rates for the whole year based on the seasonal P-I curves are shown in Fig. 3.2. The pattern follows the average number of hours of day-light occurring at Signy Island, which increases from 6 h in June to 19 h in December. The winter of 1993 was characterized by continuously changing ice conditions and late appearance of fast ice. Pack ice came in several times in Borge Bay, but fast ice was only present from 16 September till 11 November (Fig. 3.2) which slowed the increase in production rates. Only the *Desmarestia anceps* plants at 20 and 25 m depth showed, for a couple of months, a negative daily P_n, but estimated annual net oxygen production rates were still positive (Table 3.4).

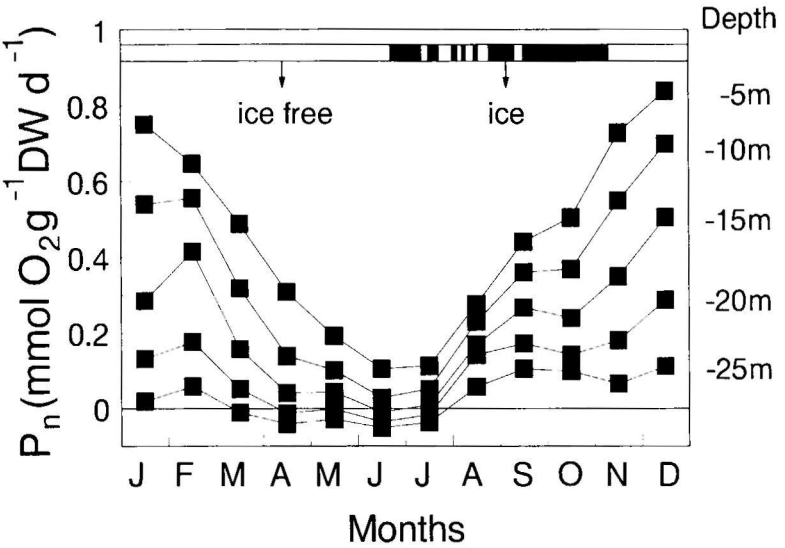

Figure 3.2. Predicted annual course of daily net production (mmol O_2 g^{-1}DW d^{-1}) for 5 m depth contours, based on the modelled equations and integrated irradiance levels per depth, taking the ice observations into account. SD increased from 4% at 5 m depth till 9% at 25 m depth

Estimated annual net production decreased from 163.8 mmol O_2 g^{-1}DW y^{-1} at 5 m depth to 10.7 mmol O_2 g^{-1}DW y^{-1} at 25 m depth. The P_n in mmol O_2 g^{-1}DW y^{-1} was recalculated to P_n(C) in g C g^{-1}DW y^{-1}, using a conversion factor of 0.012. For this conversion factor 1 mmol O_2 equals 0.032 g O_2, and 1 g O_2 equals 0.38 g C (assuming PQ = 1.00, as recommended by Rosenberg et al. (1995) for comparing results of primary production by macroalgae).

Discussion

Photosynthetic characteristics

For the first time, photosynthesis-irradiance relationships of *Desmarestia anceps* have been studied *in situ* under natural irradiance levels. The results show that *Desmarestia anceps* is well adapted to low irradiance levels and short daylengths in winter. Previous work has been carried out on laboratory cultures and in early summer on freshly sampled material (Wiencke et al. 1993, Weykam et al. 1996). The photosynthetic characteristics found in this study were lower when compared to those reported previously (Table 3.3). This may be explained by the naturally fluctuating irradiance in the field as compared to the steady irradiance levels in the laboratory, and to higher self-shading due to the usage of more plant material. Using fragments of plants can result in

wounding effects which may affect photosynthesis and respiration measurements, by for example an increase of respiration or photosynthetic rates (Arnold and Manley 1985, Hatcher 1977) Differences in chlorophyll *a* between the laboratory and field experiments could only be explained by the use of different methods of analysis or because of the different growth circumstances (field versus laboratory light conditions)

Table 3.4. Predictions of annual net oxygen production (P_n in mmol O_2 $g^{-1}DW$ y^{-1}) for *Desmarestia anceps*, based on the modelled equations for summer, winter and spring of which the photosynthetic characteristics are given in Table 3 3 Also shown are total annual irradiances (kmol m^{-2}) and percentage of surface irradiance at different depths $P_n(C)$ is P_n recalculated to g C g DW y^{-1} multiplied by a conversion factor of 0 012 (see results)

Depth (m)	Annual P_n	Annual $P_n(C)$	Annual irradiance	% of surface irradiance
surface			4 42	
below surface	200 6	2 4	2 91	65 8
-5	163 8	2 0	0 80	18 1
-10	119 6	1 4	0 34	7 7
-15	75 0	0 9	0 17	3 8
-20	37 1	0 4	0 09	2 0
-25	10 7	0 1	0 05	1 1

Seasonality in the photosynthetic characteristics was found for $P_{g\ max}$ and α Significant differences occurred between the seasons for $P_{g\ max}$, which is regarded as an adaptation to the seasonal variation of the light climate (Kirst and Wiencke 1995) The α in spring was significantly higher than in summer and winter, which might be a reflection of the adaptation of *Desmarestia anceps* to lower irradiance levels during the past winter and increased pigment content In phytoplankton research, α and P_{max} are usually expressed on a chlorophyll *a* basis In macroalgal research, a variety of choices exists and P_{max} is expressed per unit of dry weight, wet weight, chlorophyll *a* or area (Lobban 1981) Ramus (1981) recommended that for macroalgae, photosynthesis should be expressed as carbon flux per unit of chlorophyll, although the amount of chlorophyll and the rate of photosynthesis do not bear a constant relationship even at saturating irradiances In Phaeophyceae, not only chlorophyll *a* is present, but also fucoxanthin and chlorophyll *c*, which absorb wavelengths in the range 460-580 nm, depending on their protein component (Glazer 1983) That other pigments than chlorophyll *a* can be related to α was studied in *Macrocystis integrifolia* (Smith et al 1983) In this study the late summer rise in α per pigment basis was coupled to a peak in the molar ratio of fucoxanthin/chlorophyll *a*, whereas the relatively high chlorophyll *c*/chlorophyll *a* ratio in March coincided with the high initial slopes at that time A coupling between P_{max} and chlorophyll *a* was found in two other Antarctic species, *Ascoseira mirabilis* (Gomez et al

1995) and *Palmaria decipiens* (Weykam and Wiencke 1996), although in the last study a stronger correlation was found with phycobilins. Therefore, more precise information on whole pigment content is needed before chlorophyll *a* concentrations in this study can be correlated to seasonal changes in α and P_{max}, and results on a basis of chlorophyll *a* can be compared to other studies

There were two advantages of choosing self-registering incubation chambers: 1) oxygen and irradiance levels were continuously monitored under field conditions and 2) they allowed independence from the safe but strict diving and boating regulations enforced in Antarctica. Although conditions used in this study, simulated the natural environment, there were some artifacts introduced (e g chamber effects). The incubation chambers were placed in the water away from the macroalgal vegetation growing on rocky shores, preventing them from being smashed against the rocks. In contrast to kelps, species of the Desmarestiales do not grow upright towards the light, but lay flat on the ocean bottom Therefore, irradiance levels reaching the plants are similar to estimated levels based on surface irradiance and will not have an exponential relationship to canopy density as found in kelp forests (Gerard 1984) Self-shading is present in the bushy *Desmarestia anceps* plants, but shading by other species is zero as no other overstory macroalgae occur. Although the effects of waves and currents on the penetration of irradiance to greater depths were included in this approach, the effects on movements of the plant itself and therefore on the photosynthetic activity were excluded from this study by using closed incubation chambers Therefore, the photosynthetic performance may be overestimated (Wheeler 1980), especially in the first metres where waves have the strongest influence.

Daily and annual production rates

Translating photosynthesis measurements to daily production rates might have caused an overestimation, because of the optimal light conditions used. Although changing water transparencies and ice cover in winter were taken into account, most of the incidental irradiance levels in the water column were determined on calm days. As the incubation chambers could, due to weather conditions, not be deployed every day and sometimes only for a couple of hours, daily long term *in situ* light measurements are not available, and this might have resulted in overestimated irradiance levels. Continuous measurements of irradiance levels are invaluable in assessing photosynthetic responses of macrophytes as they can change drastically during the day, are variable and can show a unpredictable pattern underwater (Dunton 1994). Annual underwater irradiance levels were in this study based on the surface irradiance and incidental depth measurements Whether P-I curves can be used to predict diurnal photosynthesis in the field, based on daily irradiance, was not tested in this study, but recently more data in the literature show that photosynthesis can vary throughout the day (Hader and Schafer 1994, Hanelt et al 1993, Jassby 1978, Ramus 1981, Ramus and Rosenberg 1980).

Henley (1993) concluded in his review on measurement and interpretation of photosynthetic P-I curves in algae that P-I relationships can be very dynamic on short time scales. These differences are not detectable in field incubations and therefore it is not known how important this might be for the measurements carried out in this study

Ice conditions were not exceptional in 1993 compared to other years (Clarke et al. 1988) When ice cover became permanent in September and October a decrease in P_n occurred, especially for macroalgae growing deeper than 10 m. It is therefore believed that not only the short period of high water transparency in spring is important for macroalgae (Kirst and Wiencke 1995), but the increasing daylengths and relatively higher irradiance levels caused by higher sun elevations are important as well.

The maximum depth of occurrence for *Desmarestia anceps* based on the modelled annual net production rates was predicted at 27.7 m depth, which is comparable to the maximum depth of 30 m found in a previous study on biomass and percentage cover data of *Desmarestia anceps* (Brouwer et al. 1995). Biomass of *Desmarestia anceps* reached an average of 1.0 kg DW m^{-2} at 11 m, and only 0.1 kg DW m^{-2} at 17 m depth (Brouwer et al. 1995) At 25 m the biomass is expected to be even less, which makes the low annual production rate of 10 7 mmol O_2 g^{-1}DW y^{-1} reliable. Unfortunately, at present, no estimates of growth of *Desmarestia anceps* determined *in situ* are available. Although predictions made on depth distributions derived from laboratory photosynthetic experiments may not always be appropriate (Dunton and Tomasko 1994), based on culture studies, Wiencke (1990) estimates that a lower depth distribution of 28 ± 5 m in inshore waters and a minimum annual irradiance of 31 mol m^{-2} was needed to complete the life-cycle of *Desmarestia anceps* Therefore, *Desmarestia anceps* might occur deeper at other sites and areas, as a result of different water transparencies and weather conditions (Kloser et al 1996)

The predicted annual production rate of *Desmarestia anceps* (0.9-1.4 g C g^{-1}DW y^{-1}) at 12 m depth was higher than the modelled rate of *Macrocystis pyrifera* (0.4 g C g^{-1}DW y^{-1}), a macroalga which is closely related to Antarctic brown macroalgae (Jackson 1987), although annual irradiance levels at Signy Island (Brouwer 1996) were lower than those used in Jackson's study The difference in production might be explained by the use of different species, but might also be explained by the low respiration rates of algae in polar waters, due to a lower water temperature (Neori and Holm-Hansen 1982, Tilzer and Dubinsky 1987, Wiencke et al. 1993, this study). In phytoplankton research, it is common practice to exclude respiration from productivity calculations (Kromkamp and Peene 1995), and although the calculated productivity values will be overestimated, the error in polar waters is probably slight (Brightman and Smith 1989). For *Macrocystis pyrifera* at 12 m depth the annual respiration was 66% of the annual gross production (Jackson 1987), while for *Desmarestia anceps* it was 19-26% Although the percentage in the polar species is less than in the temperate macroalga, it is still too high for excluding respiration rates from productivity values for polar macroalgae.

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In situ photosynthesis and estimated annual production of the red macroalga *Myriogramme mangini* in relation to underwater irradiance at Signy Island (Antarctica)

Patty EM Brouwer

Abstract

For the first time, photosynthesis of *Myriogramme mangini* (Gain) Skottsberg, one of the dominant red macroalgae in the sublittoral of Signy Island (South Orkney Islands), was studied *in situ* under natural irradiance levels in specially developed incubation chambers. *Myriogramme mangini* is adapted to low irradiance levels

Water transparency varied over the year. A maximum attenuation coefficient (k_d) of 0.328 m^{-1} was reached in January, and the water was clearest in September with a k_d value of 0.079 m^{-1}. Classification of the water type on a Jerlov scale, gave water type 4 in January and II in May and June. The mean k_d value over the year was 0.158 m^{-1} and the water was classified as Jerlov's water type 1. The euphotic depths (Z_{eu}) for 1%, 0.1% and 0.01% surface irradiance levels were 29.1 m, 43.7 m and 58.3 m, respectively.

Photosynthetic characteristics were determined, with the oxygen production rates and irradiance levels measured *in situ*, using P-I curves. The initial saturation irradiance (I_k) varied significantly from 18.0 ± 1 5 µmol m^2 s^{-1} in autumn to 10.5 ± 1 8 µmol m^2 s^{-1} in early spring. Mean photosynthetic capacity ($P_{g\ max}$) ranged from 57 2 ± 1 3 µmol O_2 g^{-1}DW h^{-1} to 63.1 ± 1.6 µmol O_2 g^{-1}DW h^{-1} The photosynthetic efficiency (α) was 3.2 ± 0.2 µmol O_2 g^{-1}DW h^{-1}(µmol m^2s^{-1})$^{-1}$ in autumn and 6.0 ± 1.0 µmol O_2 g^{-1}DW h^{-1} (µmol m^2s^{-1})$^{-1}$ in early spring Compensation irradiance (I_c) was low and ranged from 2.5 to 2.8 µmol m^2 s^{-1}. Estimates of annual net production rates were 129 6 and 0.7 mmol O_2 g^{-1}DW y^{-1} at 5 m and 20 m depth, respectively A maximum depth of occurrence of *Myriogramme mangini* was predicted at 22.9 m (1.8% of the surface irradiance).

Introduction

Vertical and horizontal distribution patterns of macroalgal communities have recently been described from several sites in Antarctica (Amsler et al. 1995, Brouwer et al 1995, Chung et al. 1994, Cormaci et al. 1992, Kloser et al. 1994, 1996) On the rocky coast of the South Orkney Islands and the Antarctic Peninsula, the main contributors to the biomass of sublittoral vegetation are usually the large overstory Phaeophyta. The Rhodophyta are more abundant in species number and form the understory, or grow at sites where large Phaeophyta are not present.

Primary production studies of Antarctic macroalgae *in situ* have been few, probably because of the inaccessibility of the area and the demands of working under water. Studies of the growth of Antarctic macroalgae have utilised laboratory cultures (Wiencke 1990a, 1990b) The Rhodophyta in these studies showed a seasonal optimum in growth rate between October and December Wiencke et al (1993) studied photosynthetic characteristics of several macroalgae from Antarctica cultivated under different light and temperature regimes, while the photosynthesis and respiration of some Antarctic macroalgae collected at Signy Island were studied by Drew (1977). Weykam et al (1996) gave an overview of the photosynthetic characteristics of numerous macroalgae collected at King George Island The only seasonal photosynthesis measurements carried out *in situ* to date are on the large kelp-like brown macroalga *Himantothallus grandifolius* (Drew and Hastings 1992) and in a parallel study on *Desmarestia anceps* (Brouwer 1997). Data on seasonal photosynthetic performance of algae carried out in laboratory experiments on samples collected in the field are available from the Phaeophyta *Adenocystis utricularis* (Gutkowski and Maleszewski 1989) and *Ascoseira mirabilis* (Gómez et al 1995). Data on seasonal photosynthetic performance of Rhodophyta collected in the field are not available in the literature, although Weykam and Wiencke (1996) examined the seasonal photosynthetic performance of the endemic Antarctic alga *Palmaria decipiens* in laboratory cultures under simulated Antarctic light conditions. They found that a growth optimum under spring conditions coincided with a higher photosynthetic activity.

Since water temperature and salinity are relatively constant, and nutrient levels are generally high in Antarctic waters, light is the most important seasonal factor affecting the growth of macroalgae. Antarctic macroalgae are classified as shade-adapted because they have high photosynthetic efficiency values (α), a low compensation point (I_c) and low saturation irradiances (I_k) (Wiencke et al 1993) Antarctic macroalgae not only have to deal with strong seasonal changes in daylength, but also with ice cover in winter and phytoplankton blooms in summer To date, no underwater irradiance levels have been available for the periods of winter ice cover and summer phytoplankton blooms, both of which influence irradiance levels at greater depths.

The irradiance penetrating the water column in Antarctica undergoes large spatial

and temporal variations, caused by a variety of factors They include not only latitude, wave action at the surface, phytoplankton blooms or turbidity of the water column, but also changes in ice thickness and the structure of the ice The last in particular is determined by whether the ice is sea ice or pack ice, and whether it is frozen solid or still soft and full of holes Also important is the state of the ice surface, and especially the presence of snow, melt ponds, or drainage of melt water, for determining the amount of light penetrating the water column Snow in particular attenuates light: Palmisano et al. (1986) found for a 50 cm layer snow a transmittance of 0.01-3% of incident light, while the transmittance of a layer of 1 m sea ice will be about 20% of incident light (Maykut and Grenfell 1975). An overview of the influence of ice cover on the irradiance penetrating into the water column is given by Knox (1994), while Eicken (1992) discusses the role of sea ice in structuring Antarctic ecosystems

Myriogramme mangini (Gain) Skottsberg is one of the dominant Rhodophyta of the macroalgal vegetation of Signy Island (Brouwer et al. 1995) Aims of this study were (1) to determine the photosynthetic characteristics of *Myriogramme mangini* thalli *in situ*, (2) to study seasonality in irradiance levels under water and discuss transparency of the water column, and (3) to predict annual production rates.

Materials and methods

Study area and macroalgal material

The present study was carried out from January till November 1993 at three different sites of Signy Island (60°42'S, 45°36'W)· Factory Cove, Billie Rocks and the seawater sampling site (SW) in Borge Bay (Fig. 1 1) Factory Cove and Billie Rocks were used for measurements at shallow depths (0.5 and 5 m depth) and bad weather conditions (windspeed > 23 knots), and the seawater sampling site for deep measurements at 25 m depth and good weather conditions (windspeed ≤ 23 knots). Daylength in summer reaches a maximum of 19 h and in winter a minimum of 6 h During winter, light penetration to greater depths is limited by sea ice, which is present for on average 140 days per year, with a large year-to-year variation (Murphy et al 1995). Seawater temperature shows little seasonal variation, from -1.8°C in winter to about +0.3°C in summer, while salinity is constant at 33.9 ‰ (± 0 5) (Clarke et al. 1988). Nutrient levels in the water vary seasonally, but none routinely reach levels where they would be regarded as limiting. Minimum levels for nitrate, nitrite and phosphate are reached in summer during phytoplankton blooms, and minimum levels for ammonia in late winter (Clarke et al 1988)

Macroalgae are abundant in the sublittoral of the rocky coast of Signy Island and *Myriogramme mangini*, one of the dominant Rhodophyta at Signy Island, was found abundantly at depths of 2-14 m below mean low water (MLW) (Brouwer et al. 1995)

Myriogramme mangini is an endemic pseudoperennial species which is known from the Antarctic Peninsula, the South Shetland Islands and the South Orkney Islands (Lamb and Zimmermann 1977, Price and Redfearn 1968, Richardson 1979, Ricker 1987) This species overwinters by shedding parts of the blades and retaining the midribs. In early spring, plant material therefore consists mainly of the midribs with thin new leaves developed. Thalli (varying between 1.7-20.5 g wet weight) were sampled by SCUBA diving at Billie Rocks and either directly used in the incubation experiment or kept, for up to two days, in the laboratory with a continuous flow of seawater pumped directly from Factory Cove Table 4 1 shows the incubation sites and depths, and ranges of dry weights of the *Myriogramme mangini* thalli used in the experiment.

Table 4.1. Incubation sites and depths (m), ranges of dry weights (DW as % of wet weight) of the *Myriogramme mangini* thalli sampled at Billie Rocks at a depth of 5 or 6 m SW = seawater sampling site, FC = Factory Cove, BR = Billie Rocks, n = number of plants used

Season	Incubation site	Incubation depth	n	DW range
Autumn[1]	SW	5	4	16 2-20 4
	SW	25	4	6 9-20 9
	FC	0 5	10	20 5-25 0
Spring[2]	FC	0 5	2	20 3-23 2
	BR	5	3	13 6-19 2

[1] incubation dates 4, 7, 9 and 12 March and 27, 28, 29 and 30 April and 7 May 1993
[2] incubation dates 15, 21 and 23 September 1993

Oxygen evolution measurements in situ

Incubations *in situ* were conducted using two 13 l cylindrical self-registering closed plexiglass incubation chambers as described in more detail by Brouwer (1997) Each incubation chamber contained a 2π PAR (photosynthetical active radiation) light sensor (BPW 21, Skiltronics BV, Leeuwarden), two YSI 5739 oxygen electrodes with temperature sensors (Yellow Springs Instruments Inc , Ohio) and a custom-built stirring mechanism. Oxygen concentration, water temperature and irradiance were recorded every 90 seconds by a data logger (Seawise, Den Helder) on a scale from 0-998 units

The relationship between the gross oxygen production and the irradiance was determined by non-linear curve fitting, using the model of Platt and Jassby (1976)

$$P_g(I) = P_{g\,max} \tanh (\alpha I / P_{g\,max}),$$

where $P_g(I)$ is the gross oxygen production in μmol O_2 g^{-1}DW h^{-1} and I is the irradiance

under water in µmol m^2 s^1. The programme used was PrimProd, version 2.1 (de Hoop 1994), giving mean values with SD of the light-saturated rate of gross oxygen production ($P_{g\,max}$), the photosynthetic efficiency (α) as the initial slope of the P-I curve in µmol O_2 g^1 DW h^1 (µmol m^2 s^1)^1 and the initial saturating irradiance level ($I_k = P_{g\,max} / \alpha$). Gross production was estimated by adding the mean measured respiration (R) during the night to the measured net oxygen production (P_n). Indication of the irradiance compensation point (I_c) was obtained by plotting the modelled net oxygen production.

Winkler titrations (Grasshoff et al. 1983) were carried out in the laboratory in order to calibrate the oxygen electrodes with seawater from Factory Cove under the same temperatures as in the field. The light sensor of each incubation chamber was cross-correlated in the laboratory with a Li-cor quantum meter and sensor (LI-185B and LI-192SB, Li-cor Inc., Lincoln, USA) and results were integrated hourly in µmol m^2 s^1 Photosynthetic rates were expressed in units of µmol O_2 g^1DW h^1

Irradiance measurements

Irradiance at the surface was monitored by the British Antarctic Survey (BAS, unpublished data) using a CM 11-Pyranometer (spectral range 305-2800 nm, Kipp & Zonen, Delft). These readings were cross-correlated with those of the Li-cor quantum sensor by linear regression ($y = 1\,59\,x + 1\,63$, $r^2 = 0.98$, $n = 31$). Incidental irradiance measurements were carried out at the seawater sampling site, with the Li-cor quantum meter, to determine the percentage of surface irradiance available just underneath the water or ice surface and at 5-25 m depth, with 5 m depth intervals The sensor was mounted on a 1.5 m long arm and lowered to the depth desired, avoiding shading effects of the boat or people standing on the ice surface. Thickness of sea ice and the layer of snow covering the ice were also measured by the British Antarctic Survey. The daily surface irradiance in combination with the incidental irradiance measurements and the variation in ice present on the water surface were used to calculate irradiance levels at the different water depths Irradiance (I) at any depth (z) is a function of the intensity just below the water surface (or in this study also just below the ice surface) (I_0) and depth (z)

$$I_z = I_0\, e^{-k_d z},$$

where k_d is the attenuation coefficient.

Daily and annual production

The daily net production was calculated from the estimated average irradiance levels at a specific water depth per day using the fitted net production. Predictions of annual net oxygen production were made by multiplying the average daily net production with the number of days per month and adding these monthly data. Production measurements

carried out from March to early May and in September were used for the autumn and early spring P-I equations, respectively. As summer and winter measurements of the photosynthetic charateristics were missing, it was assumed that for estimates of annual production the autumn and early spring P-I equations covered May to October and November to April, respectively, using the changing irradiance levels through the year and interpolating for depth.

Data analysis

Significance of differences between photosynthetic characteristics of autumn and spring were tested using a t-test and a significance level set at p=0.05.

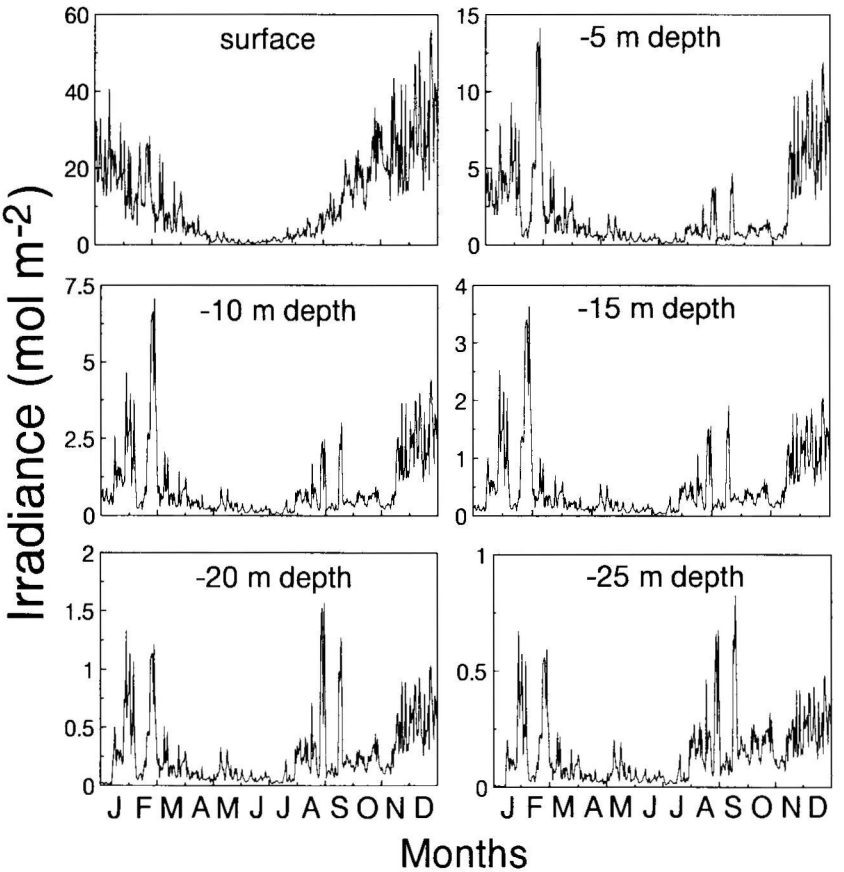

Figure 4.1. Average daily irradiance levels (PAR, mol m^{-2}) measured on the surface and recalculated from incidental depth profiles at 5 m depth intervals, from 5-25 m

Results

The estimated irradiance levels at different depths in 1993 are given in Fig. 4.1. The seasonal surface pattern becomes less obvious with depth. The total annual irradiance received on the surface (4.42 kmol m^{-2}) decreased to 0.80 at 5 m depth and 0.05 kmol m^{-2} at 25 m depth (Table 4.2), corresponding to 18.1 and 1.1% of the surface irradiance, respectively. The seasonal variation in light penetration, as percentage of the surface irradiance, and the extinction coefficient (k_d) in the water column are shown in Fig. 4.2. In January, less than 0.1% of the surface irradiance reached 25 m depth (Jerlov's water type 4, see Lüning 1990), while in May-June, when no ice was present, between 5 and 10% reached 25 m depth (Jerlov's water type II). From July until mid-September light penetration changed continuously due to the changing movements of the ice. The k_d values show the clarity of the water column. The highest k_d value (0.328 m^{-1}) occurred in January, and the lowest (0.079 m^{-1}) at the end of September. The mean k_d value calculated over the whole year based on the annual irradiance levels was 0.158 m^{-1}. The euphotic depths (Z_{eu}), for 1%, 0.1% and 0.01% of the surface irradiance, were therefore 29.1, 43.7 and 58.3 m, respectively.

Table 4.2. Predictions of annual net oxygen production (P_n in mmol O_2 $g^{-1}DW$ y^{-1}) for *Myriogramme mangini*, based on the modelled equations for autumn and early spring of which the photosynthetic characteristics are given in Table 4 3. Also shown are total annual irradiances (kmol m^{-2}) and % of surface irradiance at different depths

Depth (m)	Annual P_n	Annual irradiance	% of surface irradiance
surface		4.42	
below water/ice surface	161.9	2.91	65 8
-5	129.6	0 80	18.1
-10	90.2	0 34	7.7
-15	45 1	0.17	3.8
-20	0.7	0.09	2.0
-25	- 34.1	0.05	1 1

The autumn and early-spring P-I curves of *Myriogramme mangini* are given in Fig. 4.3, while the photosynthetic characteristics are summarized in Table 4.3. Field irradiance levels measured during these incubations ranged from 0-163 µmol m^{-2} s^{-1}. $P_{g\ max}$ was 57.2 ± 1.3 µmol O_2 $g^{-1}DW$ h^{-1} in autumn and 63.1 ± 1.6 µmol O_2 $g^{-1}DW$ h^{-1} in early spring, and the photosynthetic efficiency (α) was 3.2 ± 0.2 µmol O_2 $g^{-1}DW$ h^{-1}(µmol $m^{-2}s^{-1}$)$^{-1}$ in autumn and 6.0 ± 1.0 µmol O_2 $g^{-1}DW$ h^{-1} (µmol m^{-2} s^{-1})$^{-1}$ in early spring but differences were not significant ($p>0.05$).

Table 4.3. Photosynthetic characteristics of *Myriogramme mangini* thalli based on field incubations with a maximum irradiance level of 163 µmol m^{-2} s^{-1}. Units: $P_{g\,max}$, $P_{n\,max}$ and R (µmol O_2 g^{-1}DW h^{-1}); α (µmol O_2 g^{-1} DW h^{-1} (µmol m^{-2} s^{-1})$^{-1}$); I_c and I_k (µmol m^{-2} s^{-1}); mean values with SD in brackets. For comparison, photosynthetic characteristics determined in a previous laboratory study are included.

Parameter	This study autumn[1]	This study early spring[2]		Weykam et al. (1996) spring-summer[3]
$P_{g\,max}$	57.2 (1.3)	63.1 (1.6)	ns	143.6
α	3.2 (0.2)	6.0 (1.0)	ns	7.5 (0.8)
I_k	18.0 (1.5)	10.5 (1.8)	*	18.7 (3.7)
R	8.4 (3.4)	12.8 (6.6)	ns	35.5 (5.2)
I_c	2.8	2.5		4.5 (1.0)
$P_{n\,max}$	48.8	50.3		108.1 (44.8)

[1] Total number of plants used is 18, with P_g in duplicate at 31 irradiance levels; number of plants used for determining R is 2.
[2] Total number of plants used is 5, with P_g in duplicate at 10 irradiance levels; number of plants used for determining R is 3.
[3] Fresh material sampled at King George Island from the end of October to the start of December, and used in laboratory experiments, n = 3-4
*: significant different between autumn and early spring ($p \leq 0.05$)
ns: no significant difference between autumn and early spring ($p > 0.05$)

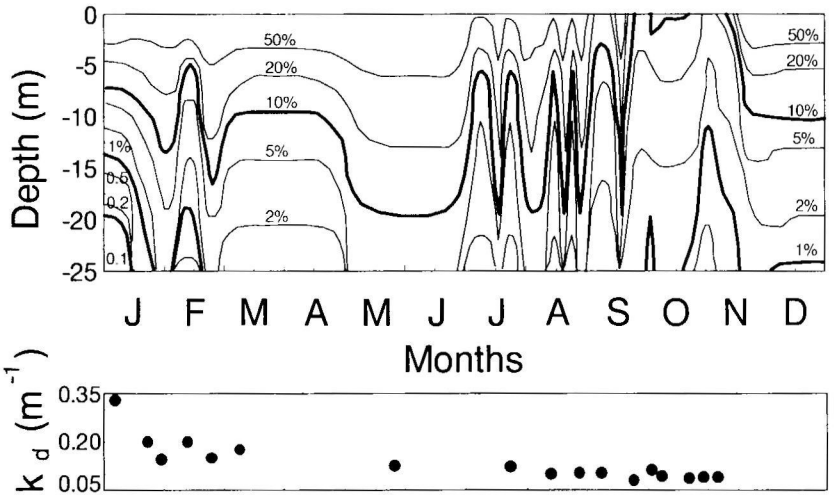

Figure 4.2. Year-round series of light penetration (%) and k_d (m^{-1}) values in Borge Bay, Signy Island, 1993

The initial saturating irradiance level (I_k) in autumn (18.0 ± 1.5 µmol m^{-2} s^{-1}) was significantly higher ($p < 0.05$) than in early spring (10.5 ± 1.8 µmol m^{-2} s^{-1}). Low irradiance

compensation points (I_c) from 2.5 and 2.8 µmol m^{-2} s^{-1} were found. Respiration rates were low and did not vary significantly between 8.4 ± 3.4 µmol O_2 g^{-1}DW h^{-1} in autumn and 12.8 ± 6.6 µmol O_2 g^{-1}DW h^{-1} in early spring. Table 4.3 also gives the photosynthetic characteristics of *Myriogramme mangini* tissue obtained from laboratory experiments with field material (Weykam et al. 1996). They found higher values for α, $P_{g\,max}$ and R, and comparable I_k values.

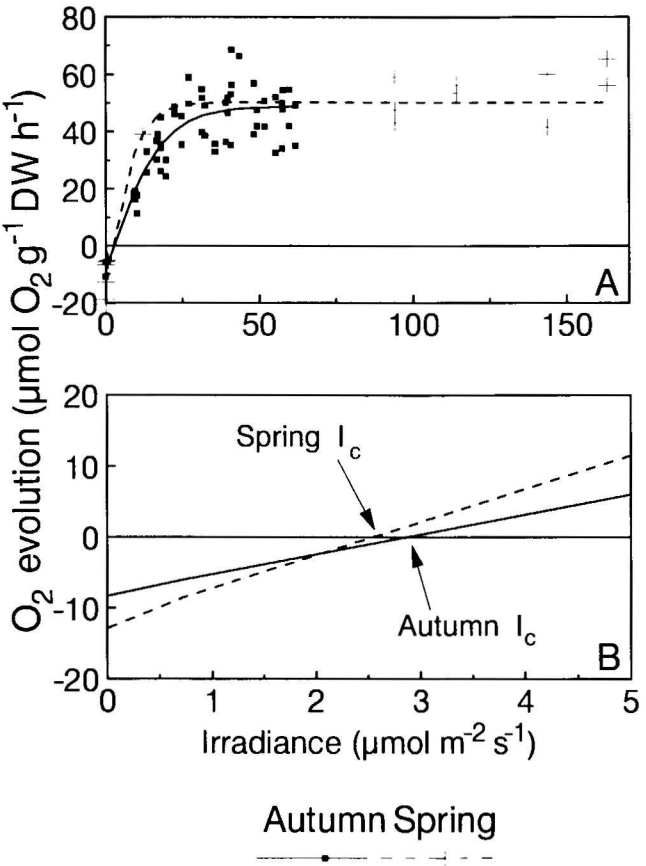

Figure 4.3. Relationship between net oxygen production rate, respiration rate (µmol O_2 g^{-1}DW h^{-1}) and the irradiance (µmol m^{-2} s^{-1}), with fitted P-I curves for autumn and early spring measurements. Individual points show the original data pooled per season (A). Enlargement of the low irradiance levels shows the modelled irradiance compensation points (I_c) for autumn and early spring (B)

The estimated daily net oxygen production rates for different depths are shown in Fig. 4.4. These were calculated from the observed mean irradiance values and the experimental data relating oxygen production to irradiance. The pattern follows the

average number of hours of day-light occurring at Signy Island, which increases from 6 h in June to 19 h in December. The winter of 1993 was characterized by continuous changing ice conditions and the late appearance of fast ice. Pack ice moved in and out of Borge Bay, but fast ice was only present from 16 September to 11 November (Fig. 4.4), which slowed down the increase in production rates. Only the *Myriogramme mangini* plants at 5 m depth showed a positive daily P_n during the whole year. Estimated annual net oxygen production rates were still positive to 20 m depth (Table 4.2), and decreased from 129.6 mmol O_2 g^{-1}DW y^{-1} at 5 m depth to 0.6 mmol O_2 g^{-1}DW y^{-1} at 20 m depth.

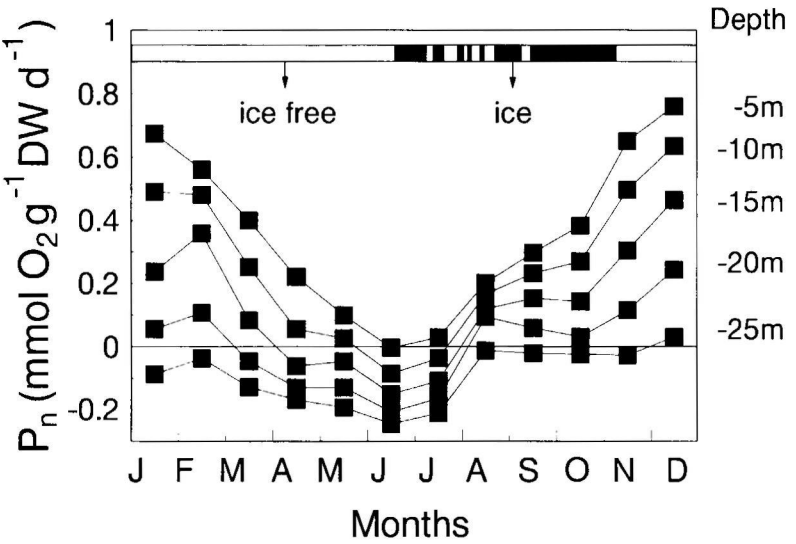

Figure 4.4. Predicted annual course of daily net production (mmol O_2 g^{-1}DW d^{-1}) for 5 m depth contours, based on the modelled equations and integrated irradiance levels per depth, taking the ice observations into account

Discussion

This study attempts for the first time to determine *in situ* photosynthetic charateristics of an Antarctic red macroalga, *Myriogramme mangini*, in relation to changes in irradiance over the year at several depths. For *Myriogramme mangini* no significant differences were found in the photosynthetic characteristics α and $P_{g\,max}$ between autumn and early spring, although the I_k in early spring was significantly lower than in autumn. Irradiance levels at 5 m depth were comparable in these periods, and were 37 and 31 mol m^{-2} $month^{-1}$, respectively. Compared to red macroalgae in other parts of the world (Dawes

and Kovach 1992, Enríquez et al 1995), I_c and I_k values were low and α high, indicating that *Myriogramme manginii* is well adapted to low irradiance levels. An earlier laboratory study using thallus parts of field grown *Myriogramme manginii* (Weykam et al. 1996) gave higher values of photosynthetic parameters, mostly refering to P_{max} and respiration, than field measurements (Table 4.3) These are almost certainly explained by the naturally fluctuating irradiance levels occurring in the field and the use of whole thalli in the field incubations. Using fragments of plants, can produce adverse effects on photosynthesis and respiration measurements (Arnold and Manley 1985, Drew 1983, Hatcher 1977). In another study of Weykam (1996), no significant differences were found in α and P_{max} between the end of winter and early summer. One explanation might be that *Myriogramme manginii* is so well adapted to low irradiance levels, that no differences in response occur between different times of the year. Another possibility is that pigments play an important role, and expressing photosynthetic characteristics on a pigment basis might give a better indication of photosynthetic performance in the field. A third option might be that the growth strategy of *Myriogramme manginii* is that of a season responder (Weykam 1996). Season responders are algae which start growth in sping and summer when they experience high light conditions, while season anticipators start growth in the winter season in response to short days (Kain 1989). No information is available on the growth strategy of this endemic species, but photosynthetic measurements carried out in the present study and by Weykam (1996) showed no significant variation in $P_{n\,max}$. Weykam (1996) concluded that the slight variation in $P_{n\,max}$ was comparable to the seasonal variation in photosynthesis of the more intensively studied red macroalga *Iridaea cordata*, which was classified as season responder. During winter, the blades of *Myriogramme manginii* degraded and only the midribs remained. The first growth of fresh young material was observed in September At this time of the year irradiance levels increased under water as a result of ice conditions. Therefore, it is well possible that *Myriogramme manginii* might act as a season responder, but more information of the growth strategy is required

A maximum irradiance level of 163 µmol m^{-2} s^{-1} was measured during the incubations, indicating that photoinhibition is unlikely to occur at Signy Island. Photoinhibition occurs in macroalgae collected from deeper water at irradiance levels above 200 µmol m^{-2} s^{-1}, while macroalgae from shallower depths are inhibited above 300-500 µmol m^{-2} s^{-1} (reviewed in Luning 1990) In Antarctica photoinhibition has been demonstrated in the eulittoral and upper sublittoral species *Palmaria decipiens* and *Adenocystis utricularis* (Hanelt et al. 1994). Similarly, in other parts of the world many macrophytes of the eulittoral and upper sublittoral showed photoinhibition during tidal emersion in the field (Hanelt 1992, Henley et al. 1992, Huppertz et al 1990). Irradiance levels at Signy Island might be low, as the sky is overcast most of the time and the average total number of hours of sunshine per month from January 1993 to November 1993 was only 79 h.

The percentage surface irradiance entering the water column is dependent critically on the nature of the surface layer, and particularly whether there is ice on the surface or not. Water transparency is expressed by the attenuation coefficient (k_d), which is determined from just underneath the water surface or ice surface to a depth of 25 m. The k_d value was high in January because of phytoplankton blooms (Clarke et al. 1988), and storms causing turbidity. Water became clearer in May when turbidity decreased. At this time, water column phytoplankton blooms disappeared and storms had less influence on the upwelling of sediments because of the presence of surface ice around the island. When sea ice was formed and remained present in October and November, k_d values decreased further. The classification of the water type according to Jerlov (1976) changed from 4 in January to II in May and June, with water types for open ocean waters numbered from I-III and water types for coastal waters numbered from 1-9 With the average k_d of 0.158 m^{-1} over the whole year, the water type can be classified as 1 (clearest for coastal waters, see Mobley 1994).

Observations on Rhodophyta at Signy Island were limited to a depth of 38 m, but some macroalgae can probably occur deeper. It must be kept in mind, however, that the present conclusions are restricted to the sites studied and depend on water transparency and irradiance level. Differences were observed in water transparencies between Borge Bay and a site on the west coast. Also Kloser et al. (1993) found higher water transparencies at the outside of Potter Cove than inside, because of high sediment loads inside. Therefore, k_d values or classifications of the water type might give more information of the sites studied, and make comparison of production rates and photosynthetic characteristics of macroalgae easier.

The pattern of daily net production (Fig. 4.4) at all depths was principally the same as the pattern of irradiance levels measured at the surface (Fig 4.1), except for the period when ice was present Only at 5 m water depth a positive balance between production and respiration was found throughout the year. Annual production was just positive at 20 m depth (Table 4.2). Extrapolation of the relationship between the annual net production and the logarithm of the annual irradiance (P_n = 49 8 ln(I) + 127.0, r^2 = 0.97), would give a zero annual net production rate for *Myriogramme mangini* at 22.9 m depth, which is at 1.8% of the surface irradiance. Wiencke (1990b) found in a culture experiment that the minimum level of irradiance needed for completing the life cycle for two other Antarctic Rhodophyta, *Iridaea cordata* and *Gigartina skottsbergii*, was at a similar level of 2% surface irradiance. In a previous study carried out at Signy Island, *Myriogramme mangini* was mainly found between 2-14 m depth but occasionally deeper (Brouwer et al. 1995). At Anvers Island (Antarctic Peninsula), Amsler et al. (1995) found a similar distribution pattern of *Myriogramme mangini* to that at Signy Island, with highest biomass for *Myriogramme mangini* at 10 m depth The depth distribution of *Myriogramme mangini* is probably determined by the topography of the sites. Shaded sites, such as under other macroalgae or between rocks and crevices, will restrict

Myriogramme mangini mainly to shallower depths, but where the overstory macroalgae are less dense, *Myriogramme mangini* might occur deeper.

Myriogramme mangini at Signy Island was one of the 24 species of Rhodophyta found. Competition for light, space and/or nutrients with other species, such as *Plocamium cartilagineum* and *Pantoneura plocamioides*, whose probability of occurrence increased towards greater depths (Brouwer et al. 1995), might well be the reason why *Myriogramme mangini* was not abundant deeper than 14 m. But as studies of competition in marine benthic algae are few and consequences and complications are still not understood completely (Paine 1990), this is only conjecture. There is a lot of work still ahead of us in understanding the whole Antarctic macroalgal community and explaining why a given species occurs at certain depths.

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Seasonal variation in growth and photosynthesis of *Himantothallus grandifolius* in Antarctica: an *in situ* study

Patty EM Brouwer

Abstract

Antarctic macroalgae are often compared with other species of the world, although little information is available on their functioning under natural conditions. In 1993 growth of *Himantothallus grandifolius*, a kelp-like Phaeophyte, was studied at two different depths using a marking technique, and photosynthesis was determined in self-registering incubation chambers. In summer, growth at a depth of 12-14 m was higher than at 26-28 m, while in winter the production rates were equal. Despite lower irradiance levels at 25 m depth no explanations could be found in the chlorophyll *a* and C, N, P contents for the occurrence of large plants at 26-28 m depth compared to those at the 12-14 m site. The low values of the photosynthetic characteristics (I_k and α) varied seasonally, and showed an adaptation to the low irradiance levels and short daylength in winter. Predictions of annual production rates based on the photosynthesis measurements predicted a maximum depth of occurrence for *Himantothallus grandifolius* of 24.9 m, while in practice they have been located at greater depth. Production rates based on the two techniques used gave different results, and the use of parts of *Himantothallus grandifolius* laminae in photosynthesis measurements is therefore discouraged, while the marking technique is recommended.

Introduction

The large brown macroalgae in the orders Laminariales and Fucales are widely recognized as important primary producers (Mann 1973). Kelp-beds function as individual and unique ecosystems with distinct food chains, often having significant ecological importance as well as economic value (Dayton 1985, Field et al. 1977, Foster and Schiel 1985, North 1971). Dieckmann et al. (1985) speculated that the Antarctic coastal ecosystems may be structured similarly to kelp-bed ecosystems elsewhere, for although true kelps do not occur in Antarctic macroalgal communities and their place is taken by the Desmarestiales (Lüning 1990). An important representative of this group is the large endemic kelp-like species *Himantothallus grandifolius* Skottsberg, which is a perennial, massive alga with a circum-Antarctic distribution. Early development of cultured *Himantothallus grandifolius* was studied by Wiencke and Clayton (1990).

Most studies on growth and photosynthesis of Antarctic macroalgae have been carried out on specimens in laboratory cultures (Wiencke 1990a, 1990b, Wiencke et al. 1993). The first study on photosynthesis of freshly sampled Antarctic macroalgae under laboratory conditions, was carried out by Drew (1977). More recently, the photosynthetic characteristics of numerous freshly sampled macroalgae, including *Himantothallus grandifolius*, were studied by Weykam et al. (1996). Measurements of seasonal photosynthetic performance of freshly sampled algae carried out in laboratory experiments, are available from the Phaeophyta *Adenocystis utricularis* (Gutkowski and Maleszewski 1989) and *Ascoseira mirabilis* (Gómez et al. 1995).

Only a few *in situ* primary production studies of Antarctic macroalgae have been performed, probably because of the inaccessibility of the area and the constraints of working under water. A year-round study of *in situ* growth and photosynthesis of adult *Himantothallus grandifolius* was carried out from 1973 till 1975 at Signy Island by Drew and Hastings (1992), who found growth rates between 1.1 and 2.1 mm d^{-1} at 6 m depth in the growing season. Unfortunately, measurements were restricted to this shallow depth, whereas *Himantothallus grandifolius* can occur till depths of 35 m (Brouwer et al. 1995). The growth rates, measured by Drew and Hastings (1992) were low compared to the mean rates of 6 mm d^{-1} found ten years later in late summer at King George Island at 25 m depth (Dieckmann et al. 1985). Furthermore, no comparison was made between production rates of shallow and deep water sites. Information of variation in chlorophyll content, either seasonal or at different depths or along the lamina, is also lacking (Drew and Hastings 1992). Recently, *in situ* measurements of photosynthesis were carried out for *Desmarestia anceps* (Brouwer 1997) and *Myriogramme mangini* (Brouwer 1996).

The aims of this study were to determine the growth of *Himantothallus grandifolius* at two different light regimes, and the photosynthetic characteristics in different seasons. Also the annual production rates were predicted at different depths in relation to the change in irradiance over the year. Furthermore, the marking and oxygen production

methods are compared and evaluated for their suitability, and it will be discussed whether C, N, P and chlorophyll *a* contents might explain the observed variance in production rates of *Himantothallus grandifolius* at the two light regimes. In general this study will contribute to a better understanding of the functioning of Antarctic macroalgae and add to the limited information presently available.

Materials and methods

Study area and macroalgal material

The present study was carried out at Signy Island, Antarctica (60°42'S, 45°36'W, Fig. 1.1) from December 1992 till November 1993. Primary production of *Himantothallus grandifolius* was determined under field conditions by measuring growth and photosynthesis By SCUBA diving, experiments were conducted at different sites: Outer Island for the growth experiment, where *Himantothallus grandifolius* occurs from 5 to 35 m depth below mean low water (MLW), and Factory Cove, Billie Rocks and the seawater sampling site (SW) in Borge Bay for the photosynthetic measurements at three different depths. *Himantothallus grandifolius* is one of the dominant Phaeophyta from the total of 36 macroalgal species found at Signy Island (Brouwer et al. 1995) and a kelp-like species forming long flat laminae, which reach lengths of several metres.

Growth measurements in situ

In order to study growth under different light regimes, two depths were chosen at Outer Island, a relatively shallow site at 12-14 m below MLW and a deeper site at 26-28 m below MLW. In December 1992, 11 laminae were randomly chosen and marked at the shallow site and 12 at the deeper site. Individual lamina were marked by putting numbered tie-straps around the stipe of the plant. Following the method of Mann et al. (1979), which is based on that of Parke (1948), twenty holes were punched, each with a diameter of 0 5 cm and separated by 2 cm along the central line of each selected lamina, starting from the place where the stipe was 2 cm wide upwards. At the start of the experiment, total length of the lamina and widths at the base, the middle and the end of the lamina, and at the 1st, 10th and 20th hole were measured

In April 1993, the start of winter, these measurements were repeated, and in addition the total length of the punched area, the maximum diameter of the holes and the length between the holes were determined. At the same time 10 laminae were sampled from both depths in the same area as the marked plants, and taken to the laboratory for determining the C, N, P and chlorophyll *a* contents at the base, middle and end of the laminae At these three positions on the laminae, an area of 5 cm x 5 cm was cut out for determination of the dry weight/fresh weight ratio (DW/FW ratio) and the ash-free dry weight (AFDW).

In October 1993, the marked laminae were collected from both sites, and transported to the laboratory for repeated measurement of all these variables.

The total area (A) of the laminae in December, April and October was estimated with.

$$A = L/2((w_b+w_m)/2) + L/2((w_m+w_e)/2),$$

where L is the total length (cm), and w_b, w_m and w_e is the width (cm) of the lamina at the base, middle and end, respectively. The punched-hole area (A_p) was determined by.

$$A_p = L_p ((w_1+w_{10}+w_{20})/3),$$

where L_p is the length (cm) of the punched-hole area, and w_1, w_{10} and w_{20} is the width (cm) of the punched-hole area at the 1st, 10th and 20th hole, respectively

The fresh tissue material cut from the laminae was dried at 60-80°C for at least 48 h to obtain a constant dry weight. Ash content was measured by determining the weight loss after combustion of sub-samples of the dry material at 550°C for at least 3 h For CNP analysis, the dried samples were ground, and organic carbon and total nitrogen determined by using a Carlo Erba NA-1500 autoanalyser following the method of Nieuwenhuize et al. (1994). Phosphorus content was measured using a strong oxidizing acid digestion (hydrochloric acid + nitric acid + perchloric acid) in a microwave oven (Nieuwenhuize and Poley-Vos 1989) followed by a colorimetric phosphate determination of the digest solution (Chen 1956). Chlorophyll *a* was measured by freeze-drying the plant material, grinding it using a ball-mill and extracting it with 90% acetone for 24 h. The amount of chlorophyll *a* was determined by high-performance liquid chromatography (Millipore Waters) according to Brown et al. (1981).

Oxygen evolution measurements in situ

Middle sections of *Himantothallus grandifolius* laminae (varying from 22 5 to 141 2 g wet weight, with estimates of absolute lamina area of 200-450 cm^2 and fractional lamina area of 5-30% of the entire thallus), different from those used in the growth experiment, were cut out and incubated for the photosynthetic measurements. Weather conditions and safety constraints on diving and boating activity sometimes inhibited direct incubation after sampling. Occasionally, lamina had to be stored under dark conditions in running seawater with equal temperatures as outside. Therefore, for adaptation to the irradiance level in the field, measurements on the lamina started only after one hour By cutting parts of plant material out of the middle of the randomly selected laminae, two cut edges were always made across the width of the laminae. Table 5.1 summarizes the incubation dates, sites and depths, sampling sites and depths, and ranges of dry weights and chlorophyll *a* contents of *Himantothallus grandifolius* tissues used in the incubations.

Table 5.1. Incubation sites and depths (m), sampling sites and depths (m), ranges of dry weights (DW as % of fresh weight) and chlorophyll *a* content (Chl *a* in mg Chl *a* g^{-1}DW) of the *Himantothallus grandifolius* parts. SW = seawater sampling site, FC = Factory Cove, BR = Billie Rocks, BaR = Bare Rock, OI = Outer Island; n is number of tissues of different laminae used

Season	Incubation site	Incubation depth	Sampling site	Sampling depth	n	DW range	Chl *a* range
Summer[1]	SW	5	BaR, OI	10, 12	6	14.8-16.8	1.2-1.6
	SW	25	BaR, BR	8, 10	6	14.3-15.6	1.1-1.6
Winter[2]	FC	0.5	BR, OI	4, 8	6	13.7-17.4	1.5-1.9
Spring[3]	BR	5	BR	8	2	14.0-14.7	2.5

[1] incubation dates: 5, 6, 13, 18, 22, 27 and 29 January 1993
[2] incubation dates: 20, 24 and 27 August 1993
[3] incubation date: 2 October 1993

Photosynthetic incubations were conducted *in situ* using two cylindrical self-registering plexiglass incubation chambers at equal depth (incubation volume = 13 litre) as described by Brouwer (1997). Each incubation chamber contained a 2 π PAR (= photosynthetically active radiation) light sensor (BPW 21, Skiltronics BV, Leeuwarden), two YSI 5739 oxygen electrodes with temperature sensors (Yellow Springs Instruments Inc., Ohio) and a custom-made stirring mechanism. Oxygen concentration, water temperature and irradiance were recorded every 90 seconds by a data logger (Seawise, Den Helder) on a scale from 0 to 998 units.

Winkler titrations (Grasshoff et al. 1983) were carried out in the laboratory in order to calibrate the oxygen electrodes with seawater from Factory Cove under ambient temperatures. The light sensor of each incubation chamber was cross-correlated in the laboratory with a Li-cor quantummeter and sensor (LI-185B and LI-192SB, Li-cor Inc., Lincoln, USA) and results were integrated hourly in µmol m^{-2} s^{-1}. Calculations of oxygen production and consumption were performed according to Brouwer (1997) and photosynthetic rates expressed in units of µmol O_2 g^{-1}DW h^{-1}.

For determination of the photosynthetic characteristics, data of the first 2 to 3 hours of oxygen evolution in the incubation chambers were used in order to avoid a possible inhibiting effect of increasing oxygen concentration on the photosynthesis (Gordon and Sand-Jensen 1990). The data were pooled seasonally to give mean summer, winter and spring estimates. Gross production of *Himantothallus grandifolius* was estimated by plotting the oxygen evolution in the incubation chambers as a function of irradiance (P-I curves) by non-linear curve fitting, using the model of Platt and Jassby (1976):

$$P_g(I) = P_{g\,max} \tanh (\alpha I / P_{g\,max}),$$

where $P_g(I)$ is the gross oxygen production in µmol O_2 g^{-1}DW h^{-1} and I is the underwater

irradiance in µmol m^{-2} s^{-1}. The programme used was PrimProd, version 2.1 (de Hoop 1994), presenting mean values with SD of the light-saturated rate of gross photosynthesis ($P_{g\ max}$), the photosynthetic efficiency (α) as the initial slope of the P-I curve in µmol O_2 g^{-1}DW h^{-1} (µmol m^{-2} s^{-1})$^{-1}$ and the initial saturating irradiance level ($I_k = P_{g\ max} / \alpha$). Gross production was estimated by adding the mean measured respiration (R) to the measured net oxygen production (P_n). The irradiance compensation point (I_c) was obtained by plotting the modelled gross oxygen production minus the respiration rate.

After incubation, part of the fresh material was frozen at -40°C for chlorophyll *a* analysis as described before.

Irradiance measurements

Irradiance at the surface was monitored by the British Antarctic Survey (BAS, Cambridge, unpublished data) using a CM 11-Pyranometer sensor (Kipp and Zonen, Delft). These readings were cross-correlated with those of the Li-cor quantum meter over a whole day by linear regression ($y = 1.59 x + 1.63$, $r^2 = 0.98$, $n = 31$). Irradiance depth profiles to 25 m depth at intervals of 5 m were made 17 times throughout the year at the seawater sampling site (SW, Fig. 1.1) using the Li-cor quantum meter. The sensor was mounted on a 1.5 m long arm and lowered to the depth desired, avoiding shading effects of the boat or people standing on the ice surface. The surface irradiance measurements from the pyranometer in combination with the incidental irradiance penetration measurements and the observations whether ice is present on the water surface or absent, were used to calculate irradiance levels at the different water depths.

Daily and annual production

For comparing the estimates of daily production from respectively the growth measurements and the oxygen production measurements, daily net production rates were expressed in g C g^{-1}AFDW. To convert mmol O_2 to g C, a conversion factor of 0.012 was used (assuming the photosynthetic quotient, PQ = 1.00, Rosenberg et al. 1995). The AFDW/DW ratio of the tissue used in the oxygen production measurements was 0.74 ± 0.02 (n = 20). Biomass data (in g AFDW) were converted to g C assuming organic carbon to be 45% of AFDW (Drew and Hastings 1992).

From the oxygen evolution experiments, daily net oxygen production was calculated from the estimated irradiance levels at depth per day and the fitted net production. Predictions of annual net oxygen production were made by multiplying the modelled daily net production by the number of days per month and summing these monthly data. Production measurements carried out in January, August and in October were used for the summer, winter and spring P-I curves, respectively. As autumn measurements of the photosynthetic charateristics were missing, it was presumed that summer period lasted from November till April.

Data analysis

In the growth experiment, differences in lengths, widths and areas of the laminae at different depths were tested, after logarithmic transformation, with a repeated measures ANOVA (as the same plants were used throughout the experiment) Differences in logarithmically transformed data of chlorophyll *a* and arcsine tranformed data of %N, %C and %P were tested with an ANOVA for time, depth and position Variation in the photosynthetic characteristics given by the model, the respiration rate and the chlorophyll *a* content were tested with an ANOVA, while differences in these variables between the seasons were determined with a Tukey-Kramer multiple comparison test Differences were considered to be significant when $p<0\ 05$

Results

Growth measurements in situ

Table 5 2a summarizes the length, width, area and percentage increase in area of the laminae determined in December (at the start of the experiment), April (at the start of the austral winter) and in October (at the end of the experiment in spring) The laminae at the shallow site were, in general, significantly longer and wider, and are therefore significantly larger in area than those from the deep site (Table 5 2b) After summer, the gain of lamina area at the shallow site was 13 8% (± 18 6) and at the deep site 24 4% (± 48 1) Standard deviations were large because of the growth differences between the laminae After winter, the loss of lamina area was higher at the shallow site than at the deep site, and part of the lamina area which was gained at the shallow site in summer was lost in winter Loss of material was caused not only by abrasion at the tip but also by rips to the laminae

Fig 5 1 shows the increase in length of the punched area The laminae grew more at the base than at the end At the shallow site, the increase in the summer period was higher than in the winter-spring period, while at the deep site the increase in the winter-spring period was greater than in the summer period The percentage increase in punched area (A_p) is given in Table 5 2a, and the lamina area from the shallow site increased significantly more than those from the deep site

Daily growth rates of *Himantothallus grandifolius* are given in Table 5 2c, after conversion of the raw data into growth rates in carbon as described in materials and methods The data show the differences in growth rates between summer period and winter-spring period, but also emphasize the equality in growth rate in the winter-spring period for the two different depths

Table 5 3 shows the chlorophyll *a* and C, N, P contents of the randomly sampled *Himantothallus grandifolius* laminae in April and punched laminae in October together with the results of the ANOVAs A strong significant difference was found in chlorophyll *a*

between the three positions on the laminae and to a lesser extent between the different months, whereas no significant difference was found between the two depths. C and P contents were significantly different between months, depth and position on the laminae, while for the N content this was only the case for position on the laminae. Significant interactions were only found for the N content for Month*Depth and Depth*Position. The C:N:P ratio determined from the average C, N and P contents of the lamina, decreased from April to October at both depths. At the shallow site the ratio decreased from 453:20:1 in April to 420:19:1 in October, while at the deep site the ratio was lower and decreased from 409:20:1 to 347:16:1.

Table 5.2. Mean values with SD in brackets of length (L in m), width (w_m in cm) at the middle of the marked *Himantothallus grandifolius* laminae, calculated total area (A in dm^2), percentage change in total area ($\%A_{gain/loss}$) at the shallow (12-14 m, n = 11) and deep (26-28 m, n = 12) site of Outer Island in December, April and October, seasonal percentage of increase in punched area (% increase A_p), total percentage of increase in punched area (total % increase A_p) (**a**), ANOVA tables with F-values shown and significant effects denoted as: * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$, ns = not significant (**b**), and average daily production (mg C g^{-1} AFDW day^{-1}) with SD in brackets in summer and winter-spring period, determined from the growth measurements and for comparable periods and depths as the oxygen evolution measurements from Fig. 5.2 (**c**)

a Site	L	w_m	A	$\%A_{gain/loss}$	% increase A_p	total % increase A_p
Shallow						
Dec	2.9 (0.1)	18.5 (5.8)	48.3 (33.5)			
April	3.3 (1.3)	20.1 (5.9)	52.5 (33.7)	13.8 (18.6)	130.3 (45.0)	
Oct	3.4 (1.2)	20 1 (5.7)	47 3 (28.6)	-4.2 (21.1)	28.4 (17.9)	194.3 (63.7)
Deep						
Dec	1.5 (0.7)	14.1 (5.0)	18.0 (15.9)			
April	1.7 (0.7)	14.9 (4 1)	20.0 (13.9)	24.4 (48.1)	33.6 (41.0)	
Oct	1.6 (0.5)	16.0 (4.4)	19.7 (11.0)	2.1 (18.5)	26.4 (19.1)	67.9 (51.3)

b	ANOVA			
	Univariate repeated measures analysis for depth:		Multivariate repeated measures analysis:	
		F-value		F-value
	L	20.255***	L*Depth	0.856^{ns}
	w_m	5.432*	w_m*Depth	0.698^{ns}
	A	14.436**	A*Depth	$0 614^{ns}$

c Site	Season	Growth rate based on growth measurements	Growth rate based on O_2 evolution measurements
Shallow	Summer	5.32 (2.32)	2.8
	Winter-Spring	0 74 (0.48)	1.0
Deep	Summer	1.24 (1.20)	-0.7
	Winter-Spring	0.60 (0.40)	-0.8

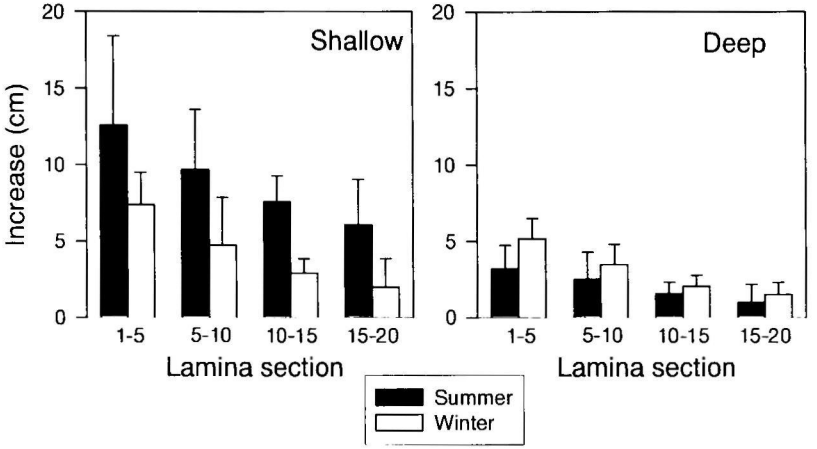

Figure 5.1. Mean increase in length in the punched area of *Himantothallus grandifolius*. 1-5 = increase in length of the first hole till the fifth hole, 5-10 = increase in length of the fifth till the tenth hole, etc. Summer is the period of December-April and winter the period of April-October

Oxygen evolution measurements in situ

Photosynthetic characteristics determined from the fitted models, between net production and respiration rates of *Himantothallus grandifolius* and the underwater irradiance, are summarized in Table 5.4 together with the statistical ANOVA and Tukey-Kramer tables. Field irradiance levels measured during these incubations ranged from 0 to 215 μmol m^{-2} s^{-1}. No significant difference between seasons was found in $P_{g\,max}$, which varied from 34.7 ± 0.9 μmol O_2 g^{-1}DW h^{-1} in summer to 44.7 ± 4.1 μmol O_2 g^{-1}DW h^{-1} in spring. However, both the photosynthetic efficiency (α) and the initial saturating irradiance level (I_k) varied significantly with season. The α in summer was significantly lower than in either winter or spring, and the winter value was significantly lower than in spring. The I_k in summer was significantly higher than in winter and spring, but no significant difference was found between winter and spring. Irradiance compensation points (I_c) were low, between 1.3 and 2.4 μmol m^{-2} s^{-1}. Furthermore, a significant variation was found in the respiration rates (R), with summer values significantly lower than in winter but not significantly different as in spring, and no significant difference between winter and spring. The chlorophyll *a* content also showed a strong significant variation, with Chl *a* in summer significantly lower than in winter and in spring, and Chl *a* in winter significantly lower than in spring.

Daily and annual production rates

The daily net production rates averaged per month for different depths are shown in Fig. 5.2. The basic pattern is dictated by the average number of hours of daylight occurring at Signy Island, which increases from 6 h in June to 19 h in December.

Table 5.3. Chlorophyll *a* (mg g^{-1}DW) and C, N, P contents (%DW) at the three positions (b = base, m = middle, e = end) of 10 randomly sampled *Himantothallus grandifolius* laminae in April and the marked *Himantothallus grandifolius* laminae in October at the shallow (12-14 m) and deep (26-28 m) sites of Outer Island. Mean values with SD in brackets (**a**), and ANOVA table of logarithmic transformed Chl *a* data and arcsine transformed %C, %N, %P data with F-values shown (**b**). Significant effects are denoted: * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$, ns = not significant

a

Site	Month	Pos	Chl *a*	%C	%N	%P
Shallow	April	b	0.9 (0.2)	36.6 (1.3)	2.3 (0.1)	0.29 (0.09)
		m	1.2 (0.3)	34.8 (1.4)	1.7 (0.1)	0.18 (0.03)
		e	0.8 (0.1)	36.3 (1.2)	1.6 (0.1)	0.20 (0.05)
	October	b	0.9 (0.2)	36.9 (1.4)	2.4 (0.2)	0.30 (0.06)
		m	1.2 (0.3)	34.6 (1.2)	1.7 (0.1)	0.20 (0.03)
		e	1.2 (0.2)	35.7 (1.6)	1.7 (0.1)	0.21 (0.05)
Deep	April	b	0 8 (0.1)	35.9 (0.9)	2.4 (0.2)	0.28 (0.05)
		m	1.3 (0.3)	34.3 (1.2)	1.9 (0.2)	0.21 (0.05)
		e	1.2 (0.4)	35.4 (1 3)	1.9 (0.2)	0 22 (0 07)
	October	b	1.0 (0.3)	35.8 (1.3)	2.2 (0.1)	0.33 (0.10)
		m	1.4 (0.3)	33.0 (0.9)	1.7 (0.1)	0.25 (0.05)
		e	1.3 (0.3)	34.1 (0.7)	1.7 (0.1)	0.24 (0.03)

b

	Chl a	*%C*	*%N*	*%P*
Month	4.801*	6.467*	1.921^{ns}	4.626*
Depth	3.397^{ns}	26.336***	3.548^{ns}	6.520*
Position	20.295***	33.041***	237.881***	30.230***
Month*Depth	0.240^{ns}	2.735^{ns}	23.921***	0.814^{ns}
Month*Position	0.610^{ns}	2.316^{ns}	0.056^{ns}	0.252^{ns}
Depth*Position	0.328^{ns}	0.222^{ns}	8.793***	0.773^{ns}
Month*Depth*Position	0.699^{ns}	0.235^{ns}	1.114^{ns}	0.013^{ns}

The winter of 1993 was characterized by continuous changing ice conditions and a late appearance of fast ice. Pack ice was present intermittently in Borge Bay in early winter, but fast ice was only present from 16 September until 11 November. This slowed down the increase in production rates in spring, presumably because of the reduced light level under the ice. Table 5.2c presents a rough estimation of the recalculated daily net production rates in mg C g^{-1}AFDW d^{-1} for comparison with the results obtained from the growth experiment.

Estimated annual net oxygen production rates were still positive at 20 m depth (Table 5.5), and decreased from 95.9 mmol O_2 g^{-1}DW y^{-1} at 5 m depth to 10.8 mmol O_2 g^{-1} DW y^{-1} at 20 m depth. Table 5.5 also shows the total annual surface irradiance (4.42 kmol m^{-2}), which decreased from 0.80 at 5 m depth to 0.05 kmol m^{-2} at 25 m depth, corresponding to 18.1 and 1.1% of surface irradiance, respectively.

Table 5.4. Seasonal variation in photosynthetic characteristics of *Himantothallus grandifolius* parts (mean values with SD given in brackets) obtained from models based on field measurements grouped per season (**a**), and one-way ANOVA and Tukey-Kramer tables of the photosynthetic characteristics per season and between seasons (**b**). Units: $P_{g\,max}$, $P_{n\,max}$ and R (µmol O_2 $g^{-1}DW\ h^{-1}$); α (µmol O_2 $g^{-1}DW\ h^{-1}$ (µmol $m^2\ s^{-1}$)$^{-1}$); I_c and I_k (µmol $m^2\ s^{-1}$); Chl *a* as chlorophyll *a* content (mg Chl *a* $g^{-1}DW$); sum = summer, win = winter, spr = spring. F-values (ANOVA) and q-values (Tukey-Kramer) are shown. Significant effects are denoted: * = $p<0.05$, ** = $p<0.01$, *** = $p<0.001$, ns = not significant

a

Season	$P_{g\,max}$	α	I_k	R	I_c	$P_{n\,max}$	Chl *a*
Summer[1]	34.7 (0 9)	1.1 (0.1)	30.2 (2.9)	2.0 (0.8)	1.8	32.7	1.4 (0.1)
Winter[2]	38.1 (0.9)	1.9 (0.2)	19 6 (2 1)	4.5 (1.5)	2.4	33.6	1.7 (0.1)
Spring[3]	44 7 (4.1)	3.1 (0.2)	14.3 (2.1)	4.2 (0.4)	1.3	40.5	2.5 (0.0)

b

ANOVA							
Season	8.417^{ns}	67.556**	22.824*	6.686*			114.785***
Tukey-Kramer							
Sum vs win	ns	6.353*	6.255*	4.844*			8.746***
Sum vs spr	ns	16.330**	9.383*	3.418^{ns}			20 995***
Win vs spr	ns	9.798*	3.128^{ns}	0.450^{ns}			14.283***

[1] total number of tissue. n = 12, with P_g in duplicate at 13 irradiance levels; for R: n = 5
[2] total number of tissue. n = 6, with P_g in duplicate at 12 irradiance levels; for R: n = 4
[3] total number of tissue. n = 2, with P_g in duplicate at 8 irradiance levels; for R: n = 2

A linear regression between the logarithm of the irradiance and the net production (P_n = 32.9 ln(I) + 94.3, r^2 = 0.99), predicts a maximum depth of occurrence of 24.9 m (corresponding to 1.3% of the surface irradiance).

Discussion

Growth measurements in situ

In this study, the growth of *Himantothallus grandifolius* was studied at two different depths. Growth at 12-14 m depth was higher than at 26-28 m depth, which can easily be explained by the higher irradiance levels at shallower depths. In contrast with the laminae of the shallow site, elongation of the laminae from the deep site was higher after winter-spring than after summer. This indicates a different growth strategy for plants growing at deeper sites, which cannot be explained by the chlorophyll *a* and C, N, P contents in this study. Alteration of the photosynthetic pigment content is one possible mechanism for increasing low-light tolerance. Reduced pigment content at low temperature can be a response among algae, and can override photoacclimation to low light, which generally increases pigment content (Henley and Dunton 1995). It is possible

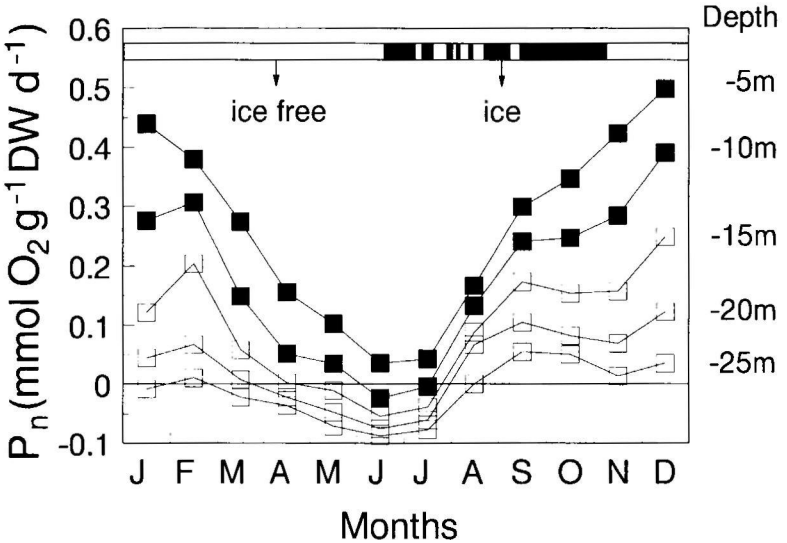

Figure 5.2. Predicted annual course of daily net production (mmol O_2 g^{-1}DW d^{-1}) for 5 m depth contours, based on the modelled equations and integrated irradiance levels per depth, taking the ice observations into account. *Dark squares* are results based on the data obtained from samples collected between 4 and 12 m depth, while the *white squares* are only predictions

that pigments other than Chl *a* or storage compounds, of which little is known today for *Himantothallus grandifolius*, contributed to more efficient growth after winter-spring at the deep site. In cultured *Laminaria solidungula* growth was observed during several months of complete darkness, provided that the plants had adequate carbohydrate reserves at the outset (Henley and Dunton 1995). The higher erosion of the laminae at the shallow site in winter might have carried away more of the tissue containing carbohydrate reserves accumulated during the previous summer (Chapman and Craigie 1978), in comparison to the deep site. Elongation rates in summer were 3.0 (± 0.8) and 0.7 (± 0.3) mm day^{-1} for the shallow and deep site, respectively. Drew and Hastings (1992) found at a 6 m site at Signy Island an elongation range of 1.1-2.1 mm day^{-1}, while Dieckmann et al. (1985) found an 2-20 mm day^{-1} at 25 m depth at King George Island. These contrasting values might be explained by the location or time period of the experiment, but also give an indication of the variability in growth at different depths, sites and locations in the Antarctic.

Total percentage increase in the punched area at the shallow site was three times as high as at the deep site, while after winter the laminae showed loss of material at the shallow site (Table 5.2a). This suggests that exposure to waves, ice-scour and possibly the grounding ice-bergs had a high impact at the shallow site, whereas at the deep site, the calmer water caused less loss of material.

Table 5.5 Predictions of annual net oxygen production (P_n in mmol O_2 $g^{-1}DW$ y^{-1}) of *Himantothallus grandifolius*, based on the modelled equations for summer, winter and spring of which the photosynthetic characteristics are given in Table 5.4. Also shown are total annual irradiances (kmol m^{-2}) and percentage of surface irradiance at different depths

Depth (m)	Annual P_n	Annual irradiance	% of surface irradiance
surface		4.42	
below water/ice surface	122.8	2.91	65.8
-5	95.9	0.80	18.1
-10	63.1	0.34	7.7
-15	33.3	0.17	3.8
-20	10.8	0.09	2.0
-25	-4.2	0.05	1.1

A current velocity of 2.9 m s^{-1} was shown to be limiting for 6 to 7 year old *Laminaria ochroleuca*, which destroyed the frond tips and progressively led to a decay of the stipe from the top (Drew et al. 1982). Current velocities at Signy Island have not been studied, but might limit growth of *Himantothallus grandifolius*. Differences in growth rates might also depend on the age of the laminae, as found for *Laminaria saccharina* (Sjøtun 1993). However, calculation of the age of the laminae, based on the data on punched area increase during the measuring period, gave a slight difference in a minimum age of 6 and 7 years for the shallow and the deep growing laminae, respectively. The laminae at the deep site must have been relatively young, because larger and wider laminae were observed at other deep sites.

As can be seen in Fig. 5.1, determination of maximum elongation of the shallow laminae was not reached within the length of the 20 holes. Assuming a linear decrease in length along the length of the laminae, extrapolation gave approximately a 10% higher increase in lamina area for the shallow site than the measured value, while the error was negligible for the deep site. It can be concluded that this method gave a good impression of growth rates, showing similar growth at the deep and shallow sites in the winter-spring period.

Oxygen evolution measurements in situ

For the first time, photosynthetic characteristics of *Himantothallus grandifolius* have been determined in different seasons. Seasonality was found for the photosynthetic efficiency (α) and the initial saturating irradiance level (I_k), which indicates adaptation to the low irradiance levels and short daylengths typical of winter. The α increased from summer to winter to spring and this might be a reflection of the adaptation of *Himantothallus grandifolius* to lower irradiance levels by increasing the pigment content. In previous laboratory studies Wiencke et al. (1993) found, in general, higher photosynthetic characteristics, although values of I_k and I_c were comparable, while Weykam et al. (1996)

found much higher I_k and I_c values but a similar α. In the present study, incubated parts of *Himantothallus grandifolius* laminae were sampled at depths between 4 and 12 m. Photosynthetic characteristics of deep growing laminae could not be determined *in situ*, because of the prevailing low irradiance levels at 25 m depth. Such data might have given an explanation for the equal biomass increase in winter for laminae growing at shallow or deep sites as found in the growth experiment. The 25 m depth incubations in this study were therefore used to determine oxygen production at low irradiance levels This species, however, grows much deeper that 25 m. Drew et al. (1982) found no satisfactory explanation for the rapid growth of *Laminaria ochroleuca* between 50 and 100 m depth based on measurements of photosynthesis and dark respiration both in the laboratory and *in situ*. However, they also used tissue with relatively large cut edges, which can produce adverse effects on photosynthesis and respiration measurements (Arnold and Manley 1985, Drew 1983, Hatcher 1977).

Daily and annual production rates

The daily production rate (Fig 5 2) shows a similar pattern as the daily hours of sunshine, with the influence of the sea ice on the production rates visible in winter and spring As ice conditions were changing in July till September, probably more light reached the macroalgae and supported greater photosynthesis compared to winters when ice is permanently present and irradiance levels are low. From mid September till mid November the ice became more solid and permanent for two months, which decreased P_n. Growth and reproduction of *Himantothallus grandifolius* occurs in a strategic annual rhythm and therefore classifies this species as a season anticipator (Wiencke 1996).

The maximum depth of occurrence for *Himantothallus grandifolius* was predicted to be 24 9 m depth, based on the annual oxygen production rates and irradiance levels However, the maximum depth of occurrence at Outer Island was found to be 35 m (Brouwer et al. 1995). An under-estimation of the annual production rate is the most likely explanation, which might be caused by overestimating respiration rates, due to large cut edges of the tissue used, or by the interpolation of P-I curves over a whole season Using the middle parts of the laminae should not have contributed to this discrepancy, as production rates were similar along the laminae, with exception of the base where net production was found to be even lower (Drew and Hastings 1992) Annual production rates were calculated from P-I curves determined in January, August and October and it was assumed that the P-I curves would adequately cover the different seasons Laboratory cultures suggested that the main growing season was from September till November (Wiencke 1990a, 1990b, Wiencke et al 1993) Therefore it is possible that $P_{g\ max}$ in summer should be higher than determined in this study However, in a parallel study, on another species of the Desmarestiales, *Desmarestia anceps*, with cut edges of only 0.5 cm, the summer P-I curve determined even later in

the season, resulted in a correct prediction of the maximum depth of occurrence (Brouwer 1997).

Incubations were limited to samples collected from 4 to 12 m depth, and therefore predicted annual production rates deeper than 12 m could be in error. The only indication of possible higher production rates at deeper sites was the higher chlorophyll *a* content in material from deeper than 25 m (unpublished data) compared to the samples used in this study. Increasing chlorophyll *a* content over water depth in *Himantothallus grandifolius* was also found by Weykam (1996)

Evaluation of methods used

A wide variety of experimental techniques has been used in macroalgal research to determine primary production. Littler and Littler (1985) reviewed these methods and included critical evaluations of each method Kemp et al (1990) suggested the use of more than one method, for each will yield specific information. The harsh environment in Antarctica will always act as a constraint on the type of research techniques which can be used, especially those involving SCUBA diving Both methods used in this study were time-consuming, but gave different types of information. The marking technique is simple and does not involve sophisticated equipment. As the plants used were very robust, no damaging effects were observed from punching the holes. Measuring all the variables under water was time consuming and therefore restricted the number of replicates. A larger number would have been more suitable as variation amongst the laminae was large Marking techniques give information of net production, whereas the O_2-evolution technique provides information of gross and net production and respiration rates Although the incubation chambers were self-registering, the oxygen electrodes needed to be calibrated regularly which involved changing membranes. After the incubation measurements, recalculation of the logged data was time consuming.

Unfortunately, the results between the two methods used were not directly comparable. One of the disadvantages of the photosynthesis measurements is that few data could be collected A better approach might have been whole day incubations with determination of production rates per day Drew and Hastings (1992) used computer simulations to estimate an annual accretion of 5.6 and 1.6 mg C cm^{-2} y^{-1} at 6 m and 11 m water depth, respectively. In the present study, much higher values of 19.7 and 12 9 mg C cm^{-2} y^{-1} at 5 m and 10 m depth, respectively, were found with the O_2-evolution technique (1 cm^2 weighed 0.0171 g (DW) and 1 mmol O_2 = 0.012 g C) The marking technique gave even higher estimates (Table 5 2c) It is clear, that for *Himantothallus grandifolius* different methods lead to different results Therefore, the data reported here suggest that for measuring production rates of *Himantothallus grandifolius*, the use of large incubation chambers, as used by Hatcher (1977) enclosing whole laminae, is strongly recommended If this is not feasible, the use of a leaf-marking technique is advised

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Decomposition *in situ* of the sublittoral Antarctic macroalga *Desmarestia anceps* Montagne

Patty EM Brouwer

Abstract

Large amounts of detached Antarctic macroalgae accumulate in hollows of the seabed, where decomposition rates of the detached macroalgae are expected to be low, caused by lack of contact of the major part of the macroalgae with the sediment. To determine decomposition rates in Antarctic waters, untreated and pre-killed *Desmarestia anceps* fronds contained in nylon net bags were studied for 10 months under natural conditions in Factory Cove, Signy Island. Physical decomposition was shown to be more important than microbial decomposition. A weight loss of 40% occurred in untreated material within 313 days, while pre-killed material almost all disappeared within 90 days. Despite the weight loss, changes in chlorophyll *a* content were negligible during the experiment. Changes in the C:N ratio and tissue N indicated low rates of microbial decomposition. Therefore, it was concluded that weight loss was mainly caused by fragmentation, and particles disappearing from the nets accounted for most of the loss of original tissue. It remains unknown as to how long nutrients stay in Antarctic macroalgal litter before they become available to the system.

Introduction

The sublittoral vegetation on the rocky shores of Antarctica comprises extensive populations of macroalgae, of which large brown macroalgae are normally the dominant species Growth occurs in the kelp-like *Himantothallus grandifolius*, a member of the Desmarestiales, from the base to approximately half-way up the length of the thallus, while erosion and decomposition take place at the frond tips (Bold and Wynne 1978, Dieckmann et al 1985) Bacteria colonize the frond tips of macroalgae and this can promote erosion (Dieckmann et al 1985, Laycock 1974) Additionally, large numbers of intact plants are lost from the sublittoral vegetation as they become detached by storms, tidal currents and ice movements These detached macroalgae can either wash ashore, as described for the Antarctic Peninsula and sub-Antarctic islands (Alkemade and van Rijswijk 1993, Bunt 1955, Crafford and Scholtz 1987, Kloser et al. 1994, Neushul 1965, Zielinski 1981), drift in the seawater and act as effective agents of dispersal for sessile invertebrates (Helmuth et al 1994) or sink to the seabed to depths below the photic zone (Fischer and Wiencke 1992, Reichardt 1987) where little is known about decomposition processes Macroalgae can store large quantities of carbon and nutrients in reserve materials, which can be mobilized to growing areas at the base of new blades (reviews in Buggeln 1983, Floc'h 1982, Schmitz 1981, Schmitz and Lobban 1976) If not grazed, macroalgae die, decompose and can become nutrient sources for the system (Hanisak 1992)

Decomposition of macroalgae in Antarctica has not been studied intensively A few reports are available studying decomposition of macroalgae stranded on Antarctic beaches (Alkemade and van Rijswijk 1993, Crafford and Scholtz 1987), but most of the research on decomposition of macroalgae *in situ* has been carried out in non-polar areas (e g Bedford and Moore 1984, Birch et al 1983, Buchsbaum et al 1991, Hunter 1976, Josselyn and Mathieson 1980, Rieper-Kirchner 1989, Smith and Foreman 1984, Williams 1984) Only Zielinski (1981) studied decomposition of Antarctic macroalgae *in situ*, and found a maximum decomposition rate for the giant kelp-like macroalga *Himantothallus grandifolius* of 0 5% per day, depending on the type of thallus, and the season

At Signy Island (60°42'S, 45°36'W), one of the South Orkney Islands, large numbers of intact detached macroalgae were observed accumulating in deeper parts of the seabed (hollows) with least water movement (Richardson 1979, own observations) and at offshore sands, peripheral to the coastal rocks (Price and Redfearn 1968), instead of stranding on beaches Although macroalgae do strand elsewhere in the Antarctic (Alkemade and van Rijswijk 1993, Bunt 1955, Crafford and Scholtz 1987, Kloser et al 1994, Neushul 1965, Zielinski 1981), this process is infrequent at Signy Island, probably because of a lack of gently sloping beaches in combination with wind and current directions In one of the hollows, 50,000 kg dry weight of detached macroalgae was

approximately estimated to have accumulated based on biomass data of a previous study on macroalgal zonation at Signy Island (Brouwer et al. 1995) This might be an over-estimation as the weight is based on living attached macroalgae, and the exact area of macroalgae covering the bottom of the hollow is unknown. It does indicate, though, that these large numbers of intact detached macroalgae could well be an important source of nutrients, and sublittoral decomposition of macroalgae might well be an influential process in the ecosystem of Signy Island.

Several factors can slow down decomposition rates (Gabrielson et al. 1983), one of which was believed to be low temperature (Carpenter and Adams 1979, Hanisak 1992, Haxen and Grindley 1985) Investigations in Antarctic waters, however, have shown high numbers and production of water column bacteria, and an activity of heterotrophic bacteria adapted to the prevailing low temperatures (reviewed by Knox 1994). Studies on marine sediments at Signy Island have also shown high populations of bacteria (Tanner and Herbert 1981) and rates of benthic microbial activity as high as those reported for other sediments at much higher environmental temperatures (Nedwell et al. 1993). So far, no data are available in the literature on microbial activity on intact detached Antarctic macroalgae that are barely in contact with the sediment, which precedes the process of decomposition of macroalgae particles by bacteria in the sediments.

Decomposition *in situ* of one of the dominant macroalgal species, *Desmarestia anceps*, has been studied in order to determine the decomposition rate and to assess the timescale over which stored carbon and nutrients of the detached macroalgae might be released to the marine ecosystem at Signy Island Based on the observed high biomass of detached macroalgae in the hollows, the working hypothesis was that rates of macroalgal decomposition *in situ*, and hence the rate of nutrient release from the detached macroalgae, would be slow.

Materials and methods

Study area

Thirty-six species of macroalgae were identified on the rocky shores of Signy Island (Brouwer et al 1995) Observations on intact detached macroalgae were carried out in Borge Bay using SCUBA diving, and accumulations of detached macroalgae were mainly found in deeper parts (hollows) of the sea bed One of these hollows covered an area of approximately 300 x 200 m and reached depths of 20-29 m below mean low water (MLW). The hollow is marked as SW (seawater sampling site) in Fig. 1.1. The area was completely covered with a mass of intact detached macroalgae reaching a maximum thickness of 0.75 m. The majority of detached species were the large brown macroalgae *Himantothallus grandifolius* Skottsberg, *Desmarestia anceps* Montagne and

Desmarestia menziesii J Agardh (Desmarestiales), and the red macroalgae *Plocamium cartilagineum* (Linnaeus) Dixon, *Myriogramme mangini* (Gain) Skottsberg and *Pantoneura plocamioides* Kylin. Based on the contribution to biomass of the different species of the macroalgal vegetation in Borge Bay (Brouwer et al. 1995), *Desmarestia anceps* was chosen for the *in situ* litter decomposition experiment. Because of safety constraints on SCUBA diving activities and accessibility of the area in most weather conditions, this experiment was carried out at Billie Rocks at a maximum depth of 12 m below MLW (Fig 1.1).

Decomposition in situ

Desmarestia anceps fronds were collected from attached living plants on 15 December 1992 at a depth of 6-8 m below MLW at Billie Rocks. Parts of macroalgae can continue to grow in nylon net bags (Josselyn and Mathieson 1980) and, therefore, the experiment was carried out on untreated and pre-killed fronds. Untreated fronds were used to study the natural process of disappearance, senescence and decomposition in detached material, while pre-killed fronds provided a more defined start to the decomposition process and accelerated decomposition. *Desmarestia anceps* fronds were killed by placing them in a seawater bath of 50°C for 10 to 15 minutes (Smith and Foreman 1984). This process caused a wet weight loss of 13 4% of the *Desmarestia anceps* fronds, due to loss in water content The surfaces of the untreated and pre-killed fronds were dried by gently pressing the fronds between tissues Both untreated and pre-killed fronds were cut or sorted into 72 portions of 30 g wet weight. The portions were placed into 15 x 15 cm nylon net bags with 1 mm mesh size The bags were sewn shut with nylon thread and fixed onto nylon ropes fastened to four 1.2 x 1.2 m PVC frames (ø 4.0 cm) Each frame held 36 (6 x 6) bags and was anchored to the sediment with iron pegs at a depth of 12 m below MLW at Billie Rocks The frames holding the bags with untreated and pre-killed *Desmarestia anceps* fronds were placed in the field on 19 December 1992 and 25 December 1992, respectively. The underside of the bags rested on the sediment. Drifting macroalgae covering the frames during the experiment were removed from the site weekly. Collections of the bags containing untreated fronds were made every calendar month. At the start of the experiment this monthly interval was also used for the pre-killed fronds, but after a rapid decrease in biomass in the 1st month the sampling frequency for pre-killed material was shortened to weekly intervals.

On each sampling date, five bags of the untreated and five of the pre-killed material were selected randomly, cut loose from the nylon ropes, placed into individual plastic bags and brought to the surface in nylon net bags The bags were transported to the laboratory in buckets filled with seawater and stored in the buckets at 0°C until analysis that same day.

The contents of the bags were carefully washed in seawater and the macrofauna, mainly amphipods, was removed. For collecting the pre-killed *Desmarestia anceps*

particles, sediment sieves (mesh size 2, 1 and 0.5 mm) were used. The wet weight was measured and sub-samples were dried at 60-80°C for at least 48 h to obtain a constant dry weight. Part of this dry material was stored in plastic pots of 7.5 ml for later analysis of C, N and P contents. Ash content was measured by determining the weight loss after combustion of sub-samples of the dry material at 550°C for at least 3 h

In non-polar regions, macroalgal biomass is consumed by grazers and is thought to be decomposed and finally mineralized in detritus food chains by bacteria, fungi and small invertebrate detrital feeders (reviews in Barnes and Mann 1980, Mann 1982), a process that can be monitored by determination of the decreasing chlorophyll content (Bianchi et al 1988, Schmidt 1980, Twilley et al. 1986). Part of the fresh material was therefore frozen at -40°C for later chlorophyll analysis. Unfortunately, for the pre-killed material this was only possible until day 48 as not enough material was available later on to determine ash, C, N, P and chlorophyll contents.

Chemical analyses

The dried samples were ground using a ball-mill. Organic carbon and total nitrogen were determined using a Carlo Erba NA-1500 autoanalyser following the method described by Nieuwenhuize et al (1994) Phosphorus content was measured using a strong oxidizing acid digestion (hydrochloric acid + nitric acid + perchloric acid) in a microwave oven (Nieuwenhuize and Poley-Vos 1989) followed by a colorimetric phosphate determination of the digest solution (Chen 1956).

Analyses of the chlorophyll content of the frozen (-40°C) samples were done by freeze-drying the plant material, grinding it using a ball-mill and extracting it with acetone for 24 h. The solution was then centrifuged for 5 min and the amount of chlorophyll *a* was determined by high-performance liquid chromatography (Millipore Waters) according to the method of Brown et al. (1981).

Environmental variables, such as temperature and nutrient concentrations (PO_4, NH_4, NO_3 and NO_2) in the water column, were monitored by the British Antarctic Survey (BAS, Cambridge, unpublished data) at the seawater sampling site (SW) in Borge Bay (Fig. 1 1). Techniques are described by Clarke et al (1988)

Presentation of results

Means of the data are presented with standard deviation (SD), and differences in time and treatment of the material were tested for significance, after arcsine or logarithmic transformation, using an analysis of variance (ANOVA, significant when $p<0$ 05).

Results

Temperature and nutrient concentrations

Temperature and nutrient concentrations in the water column during the experiment are summarized in Fig. 6.1. A maximum temperature of +0.55°C was reached in summer and a minimum of -1.84°C in winter. Nitrate and phosphate concentrations showed lower values in the summer period from November to March and varied from 14.9 to 28.7 µM and 1.19 to 2.13 µM, respectively. Ammonium was reduced to levels below detection limits in winter and a maximum of 3.17 µM occurred in April. Nitrite concentrations varied between 0.21 and 0.38 µM.

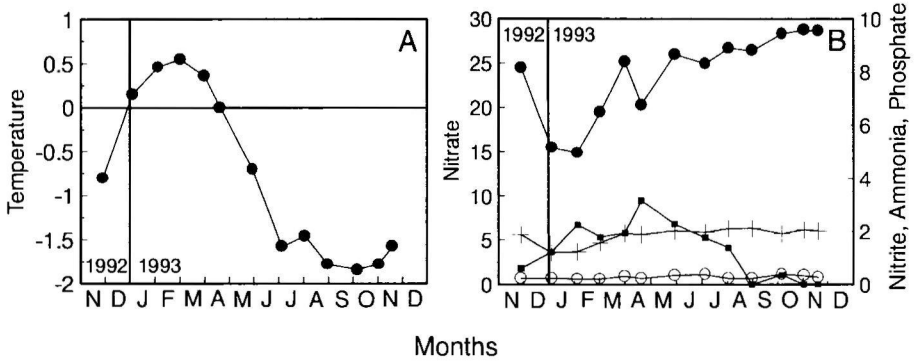

Figure 6.1. Seawater temperature (°C) (A) and nutrient concentrations (µM) (B) measured at site SW (seawater sampling site), Borge Bay, Signy Island, November 1992 to November 1993. Temperature data are mean values (SD<0.02°C) of triplicate measurements on one day. Symbols of nutrient concentrations: ● Nitrate (NO_3), O Nitrite (NO_2), ■ Ammonium (NH_4), + Phosphate (PO_4) (source: British Antarctic Survey, Cambridge)

Weight loss and changes in ash content

Both untreated and pre-killed *Desmarestia anceps* showed a significant loss in ash-free dry weight (g AFDW) with time (Fig. 6.2, $F = 6.28$, $p<0.001$; $F = 83.15$, $p<0.001$, respectively), but followed different patterns. While the biomass of untreated material remained relatively stable for a long time, the biomass of pre-killed material decreased rapidly. No weight loss was noticeable during the first period of 144 days in the untreated material, and at the end of the experiment, after 313 days, 60% of the initial weight still remained (Fig. 6.2A). The decomposition rate after 144 days was 0.24% day^{-1}. Pre-killed material showed a rapid decline to 93% of the original AFDW with a loss of 1.69% day^{-1} (days 0-55), followed by a period of relatively slow weight loss of 0.13% day^{-1} (days 55-85) (Fig. 6.2B). The relative ash content in dry weight of the samples showed, for both untreated ($F = 3.85$, $p<0.001$) and pre-killed ($F = 5.59$, $p<0.001$) material, a slight but significant increase from 25 to approximately 30% (Fig. 6.2).

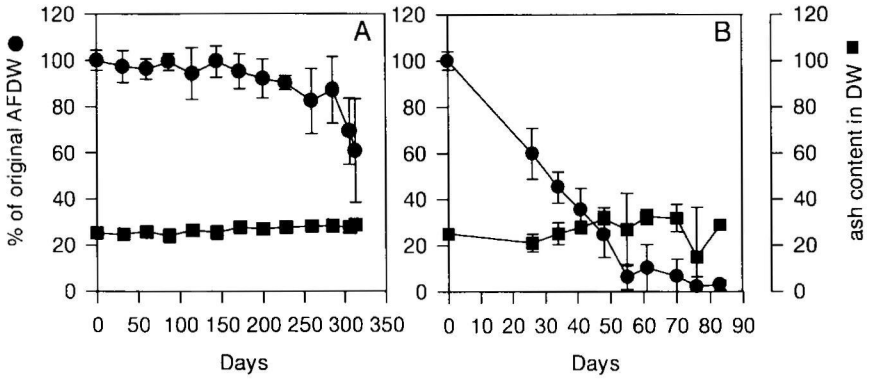

Figure 6.2. Percentage of ash-free dry weight (AFDW) and ash content in dry weight over time for untreated (A) and pre-killed (B) *Desmarestia anceps*. Day 0 as given in Table 6.1. Data are mean values (± SD) of five bags

Carbon, nitrogen and phosphorus contents

In Figs. 6.3-6.5, the relative losses of carbon, nitrogen and phosphorus, and percentages of C, N and P in tissue (DW) are presented. The significant losses in C, N and P (gr) of both untreated (C: $F = 6.51$, $p<0.001$; N: $F = 5.75$, $p<0.001$; P: $F = 2.87$, $p<0.01$) and pre-killed (C: $F = 12.89$, $p<0.001$; N: $F = 10.93$, $p<0.001$; P: $F = 18.58$, $p<0.001$) material showed a similar pattern to their weight losses (Fig. 6.2). Changes in percentage C and N in tissue of untreated material (C: $F = 4.94$, $p<0.001$; N: $F = 8.04$, $p<0.001$) and C, N and P in tissue of pre-killed material (C: $F = 4.41$, $p<0.001$; N: $F = 3.10$, $p<0.01$; P: $F = 2.48$, $p<0.05$) were significant in time, with the exception of percentage P in tissue of untreated plant material (P: $F = 1.77$, $p = 0.08$). For untreated material the average carbon, nitrogen and phosphorus percentages in tissue, during the length of the experiment, were 35%, 3% and 0.7%, respectively (Figs. 6.3A-6.5A). Untreated material showed a slight increase in the percentage of original C, N and P at the start of the experiment (Figs. 6.3A-6.5A). Pre-killed material showed a decline of 36% carbon in tissue to 29%, while nitrogen and phosphorus contents averaged 2.5% and 0.1% respectively (Figs. 6.3B-6.5B).

Pre-killing plant material caused significantly lower percentages of C and P in the tissue (C: $F = 9.87$, $p<0.01$; P: $F = 195.29$, $p<0.001$) and significantly higher N in the tissue ($F = 14.80$, $p<0.001$) compared with untreated *Desmarestia anceps* material over corresponding sampling days. Differences between the two treatments of C and N in tissue were low compared with the loss of approximately 85% of P in the tissue of pre-killed material (Fig. 6.5).

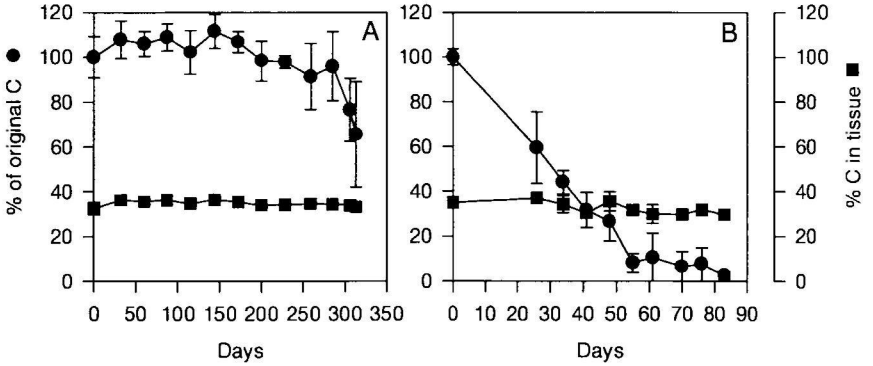

Figure 6.3. Percentage carbon in tissue and loss of carbon with time based on dry weight for untreated (A) and pre-killed (B) *Desmarestia anceps*. Day 0 as given in Table 6.1. Data are mean values (± SD) of five bags

C:N, N:P and C:P ratios

The initial ratio of carbon, nitrogen and phosphorus for the elementary composition of untreated *Desmarestia anceps* at the start of the experiment was 200C:13.5N:1P. Mean C:N, N:P and C:P ratios are presented in Table 6.1. In untreated material no significantchanges with time were found for the C:N, N:P and C:P ratios ($F = 6.74$, $p = 0.39$; $F = 0.81$, $p = 0.64$; $F = 1.32$, $p = 0.24$). Pre-killed material showed a significant decrease of the C:N ratio from 17.5:1 to 13.1:1 ($F = 5.58$, $p<0.001$), while the N:P ratio increased significantly from 36:1 to 81:1 ($F = 2.60$, $p<0.05$). The C:P ratio did not show a significant change, increasing from 620:1 to 920:1 ($F = 1.16$, $p = 0.35$).

On corresponding sampling dates during the first 85 days of the experiment, significantly different N:P ($F = 88.57$, $p<0.001$) and C:P ratios ($F = 152.80$, $p<0.001$) were found in pre-killed *Desmarestia anceps* compared with untreated *Desmarestia anceps*, while no significant difference was found in the C:N ratio ($F = 3.49$, $p = 0.07$).

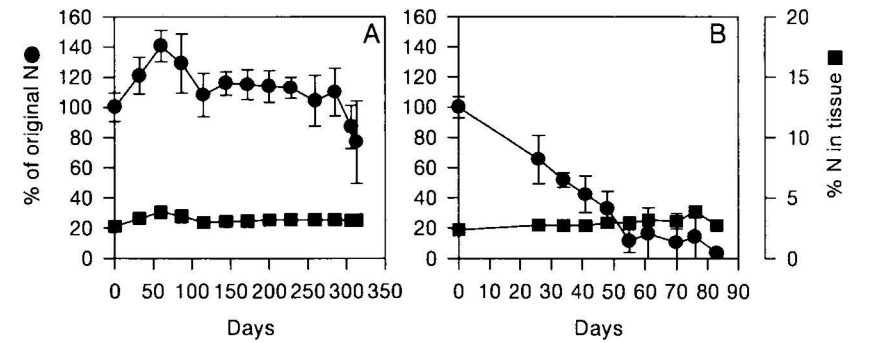

Figure 6.4. Percentage nitrogen in tissue and loss of nitrogen with time based on dry weight for untreated (A) and pre-killed (B) *Desmarestia anceps*. Day 0 as given in Table 6.1. Data are mean values (± SD) of five bags

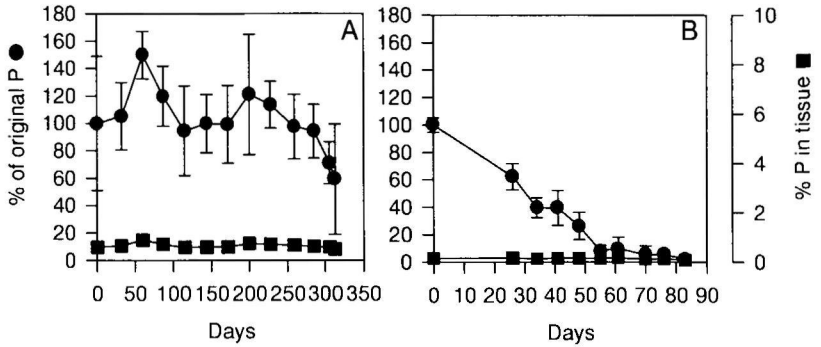

Figure 6.5. Percentage phosphorus in tissue and loss of phosphorus with time based on dry weight for untreated (A) and pre-killed (B) *Desmarestia anceps*. Day 0 as given in Table 6.1. Data are mean values (± SD) of five bags

Chlorophyll a

Neither untreated nor pre-killed material of *Desmarestia anceps* showed significant variation with time in chlorophyll *a* content (Table 6.1; $F = 1.45$, $p = 0.18$; $F = 2.50$, $p = 0.08$).

Discussion

Based on the enormous quantities of detached macroalgae found in hollows of the seabed, we expected to find low decomposition rates with a slow release of nutrients leaching from the plant material. The findings of this study support these expectations. After 313 days, 60% of the initial weight of the untreated macroalgae remained in the bags. Ninety-seven percent of the biomass of pre-killed material disappeared from the bags within 90 days. Release of nutrients is primarily related to an overall decrease in weight and, secondly, to selective leaching, as shown, for example, in C:N:P ratios. A significant decrease in C:N ratios was found in pre-killed *Desmarestia anceps* material.

Decomposition consists of different processes, including physical decomposition where physical factors like waves and currents cause fragmentation and loss of original plant material, and microbial decomposition causing loss of biomass due to continuous sloughed-off tissue, degradation of large molecules into nitrogen-containing, but decay-resistant complexes, and leaching of soluble compounds. The question is whether both of these processes are involved in this decomposition experiment or only one of them.

The decomposition rate of untreated *Desmarestia anceps* fronds seemed to be very low compared with the decomposition of pre-killed material, as it took 144 days before the untreated material began losing weight. On the other hand, it might be

possible that, during the first months of the experiment, environmental circumstances (for example, light conditions and temperature) could have allowed growth in untreated *Desmarestia anceps* fronds, and that no decomposition occurred. Although this experiment started after the growth optimum (between September and December, found in a culture study of 1-year-old plants of *Desmarestia anceps*, Wiencke 1990), growth might still occur under natural field conditions. The time of year at which the experiment was initiated might well have had an influence on the results. The intention of this study was to achieve an impression of the natural disappearance of macroalgal litter out of the system. Therefore, the start of the experiment was chosen to be summer, when most macroalgae become detached due to storms and tidal currents From day 144, untreated material decomposed at 0.24% per day The amount of biomass decrease in untreated *Desmarestia anceps* fronds in the period between days 150 and 313 seemed to occur in pre-killed material within 40 days.

Table 6.1. C N, N P and C P ratios and chlorophyll *a* content (Chl *a*) of *Desmarestia anceps* based on dry weight (mg g DW) during the experiment Day 0 for untreated *Desmarestia anceps* was 19 December 1992 and for pre-killed *Desmarestia anceps* 25 December 1992 Data are mean values (± SD) of five bags IM = insufficient material to enable assay

Day number	C N	N P	C P	Chl *a*
Untreated *Desmarestia anceps*				
0	14 5 ± 1 2	13 5 ± 7 2	200 ± 119	1789 ± 208
34	12 9 ± 0 7	13 2 ± 4 3	170 ± 55	1713 ± 57
60	10 9 ± 0 5	10 3 ± 0 9	112 ± 13	1755 ± 223
85	12 4 ± 1 7	11 8 ± 0 9	146 ± 22	1981 ± 151
115	13 7 ± 1 1	13 2 ± 3 1	182 ± 49	1462 ± 272
144	13 9 ± 0 4	13 1 ± 2 8	182 ± 39	1531 ± 126
172	13 4 ± 0 7	13 7 ± 5 2	183 ± 66	1513 ± 332
200	12 4 ± 0 5	12 1 ± 6 5	150 ± 79	1565 ± 211
228	12 5 ± 0 5	11 0 ± 1 9	138 ± 21	1593 ± 113
259	12 6 ± 0 4	11 9 ± 2 2	150 ± 25	1750 ± 267
285	12 5 ± 0 4	13 1 ± 3 1	164 ± 40	1601 ± 372
306	12 6 ± 0 4	13 6 ± 3 1	172 ± 43	1583 ± 301
313	12 3 ± 0 3	17 2 ± 5 9	212 ± 74	1765 ± 539
Pre-killed *Desmarestia anceps*				
0	17 5 ± 1 7	35 9 ± 2 2	625 ± 43	1308 ± 270
26	15 8 ± 0 4	37 5 ± 3 5	592 ± 69	1481 ± 344
34	14 9 ± 2 1	47.7 ± 6 6	710 ± 111	1755 ± 240
41	13 3 ± 1 1	38 7 ± 2 6	513 ± 41	1731 ± 336
48	14 1 ± 0 4	46 5 ± 10 3	655 ± 130	1760 ± 309
55	12 9 ± 2 1	48 8 ± 8 1	618 ± 72	IM
60	11 0 ± 1 5	48 6 ± 19 1	544 ± 224	IM
70	11 7 ± 2 4	66 6 ± 7 1	779 ± 201	IM
76	9 7 ± 0 8	80 7 ± 45 2	765 ± 372	IM
85	13 1 ± 0 8	69 0 ± 40 9	916 ± 521	IM

This could mean that the overall decomposition time could be less than 1 year and macroalgal material could be completely recycled within 1 year. This decomposition time of *Desmarestia anceps* fits into the calculated time interval of another Antarctic macroalga *Himantothallus grandifolius*, where 200-1000 days were necessary for complete decomposition of fresh material, dependent on the season (Zielinski 1981)

Loss of macroalgal biomass in both treatments gave no direct indication for the processes of decomposition involved in this study Microbial decomposition of macroalgal material is usually characterized by a decreasing C.N ratio (Reichardt and Dieckmann 1985, Rieper-Kirchner 1989), but this seems to be an assumption based on results from mainly vascular plants Contradictory results were found in several macrophyte studies (Rice and Tenore 1981, Rieper-Kirchner 1989, Twilley et al 1986), and it was concluded by Rieper-Kirchner (1989) that, in general, the C.N ratio of North Sea macroalgae decreased after a long stay in the sea According to Hunter (1976), nitrogen enrichment of decomposing plant material is a phenomenon that occurs in terrestrial, freshwater and marine environments, and is due to an increase of nitrogen-containing but decay-resistant compounds (Melillo et al 1984, Rice 1982, Wilson et al. 1986a, 1986b) The significant decrease in C N ratio and the significant increase in tissue N found for pre-killed *Desmarestia anceps* might therefore be an indication of microbial decomposition

In contrast to the findings mentioned above, no indication of microbial decomposition was found in the chlorophyll content of the algal material The chlorophyll content remained stable during the experiment. Stability of chlorophyll in sediments can be caused by anoxic conditions (Sun et al 1993) The excessive accumulation of detached macroalgae can lead to a build-up of organic material to the extent that anoxic conditions may develop in the sea floor sediments (Castilla 1985) Whether anoxic conditions occurred in this experiment is uncertain, and one unproven possibility is that pre-killing macroalgal material stabilizes chlorophyll. Another possibility is that too few data are available on the chlorophyll of pre-killed material to form conclusions There was no evidence that the macrofauna present in the bags had an influence on the weight loss of the macroalgal material This lack of grazing activities could also be indicative of a stable chlorophyll content (Bianchi et al. 1988)

Based on the chlorophyll content and the C:N ratio of the macroalgal material, it must be concluded that material of *Desmarestia anceps* leaving the bags consisted mainly of original tissue and that microbial decomposition of macroalgal material was less important than physical decomposition Particles of *Desmarestia anceps* and *Desmarestia menziesii* have been detected in sediment traps from the King George basin and in the sediment of the Bransfield Strait down to depths of almost 2000 m (Fischer and Wiencke 1992, Reichardt 1987) This supports the results of the present study, which indicate a low microbial decomposition rate in the water column. The main effect of pre-killing algal material seemed to be a rapid degradation to particles smaller

than the mesh size of the litter bags (<1 mm) and a loss of approximately 85% of tissue phosphorus. Killing the macroalgal material must have made the cellular phosphorus more accessible for micro-organisms, made the cell walls more permeable or even disrupted the cell walls completely, and stimulated leaching.

Environmental conditions at Signy Island are characterized by low water temperatures with seasonal variation and nutrient concentrations that show depletion during phytoplankton blooms in December-February (Fig. 6.1, Clarke et al. 1988). It is unlikely that the relatively small changes, of approximately 2°C in water temperature, and in nutrient concentrations in the surrounding seawater of Signy Island had an effect on the decomposition rate. On the contrary, a recent study at Signy Island showed at times, in summer, a very high microbial activity in sediments, not limited by low temperature but rather by the seasonal availability of organic matter (Nedwell et al. 1993). Numbers and production of water column bacteria in the Southern Ocean have been found to be considerable by several investigators (reviewed by Knox 1994). Gibson et al. (1990) found low bacterial numbers in winter, suggesting that little growth of bacteria occurred beneath the sea-ice. In summer, low decomposition rates of macroalgae might well be caused by the preference of water column bacteria for sea-ice microalgae or phytoplankton.

This study has documented different aspects of decomposition of Antarctic macroalgae, namely loss of biomass, changes in C:N:P contents/ratios and chlorophyll *a* content. It is possible that choice of location, water depth, lack of direct contact with the sediments that are known to be rich in bacteria, lack of direct mechanical abrasion by wave action on plants deposited on the sea-bed, and mesh size of the bags have influenced the results. Environmental factors might well differ between hollows in the sea-bed and the relatively shallow area at Billie Rocks. The influence of physical factors such as waves and currents are expected to be less in hollows and the deeper parts of the sea-bed (Seymour et al. 1989) and can therefore cause lower physical decomposition rates. Whether or not microbial and grazing activities will be higher in deeper waters has yet to be studied, but it seems likely, as the ash content in dry weight increased in a decomposition experiment of *Himantothallus grandifolius* at 25 m depth (Zielinski 1981). Laboratory experiments studying bacterial degradation of Antarctic macroalgae did indicate that the conversion of artificially generated macroalgal debris to detritus is comparable to the conversion in temperate regions, with decreasing C:N ratios, the same rate of bacterial colonization and the same bacterial density (Reichardt and Dieckmann 1985).

On the results of this experiment, it must be concluded that the dominant process in decomposition of large parts of detached *Desmarestia anceps* material, hardly touching the sediments, was physical decomposition. Apparently, the microbial decomposition rate was low compared to the contribution of physical decomposition. Leaving the bags, the majority of macroalgal particles must have remained intact. Whether the particles

floated away, remained in the system or became incorporated into the sediment by bottom fauna is an open question at present. Eventually macroalgal particles will be decomposed due to microbial activity, but how fast nutrients are recycled to the Antarctic coastal and deep-water system has yet to be discovered.

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General discussion

In the last decade, many people have gained a lot of interest in Antarctica. This nearly unexplored white continent attracts not only a variety of researchers, but also tourists. For entering the area of the Antarctic Convergence, strict rules and regulations have to be followed to preserve this nearly untouched area as good as possible for the next 50 years.

Despite the richness of species living underwater in the Antarctic, macroalgal research has been limited, and is even today mainly restricted to areas in the surroundings of research stations. One of the reasons why Antarctic macroalgae are not well studied *in situ* are the extreme conditions which often limit the work, but also the involvement of SCUBA diving. Despite people's expectations an abundant macroalgal vegetation can be present along the Antarctic coast, with a decreasing number and biomass of macroalgae towards higher latitudes. The present study carried out at Signy Island is the most detailed *in situ* study of Antarctic macroalgae known today, covering aspects of biomass and zonation patterns, production rates and decomposition rates of dominant species (summarized in Fig. 7.1).

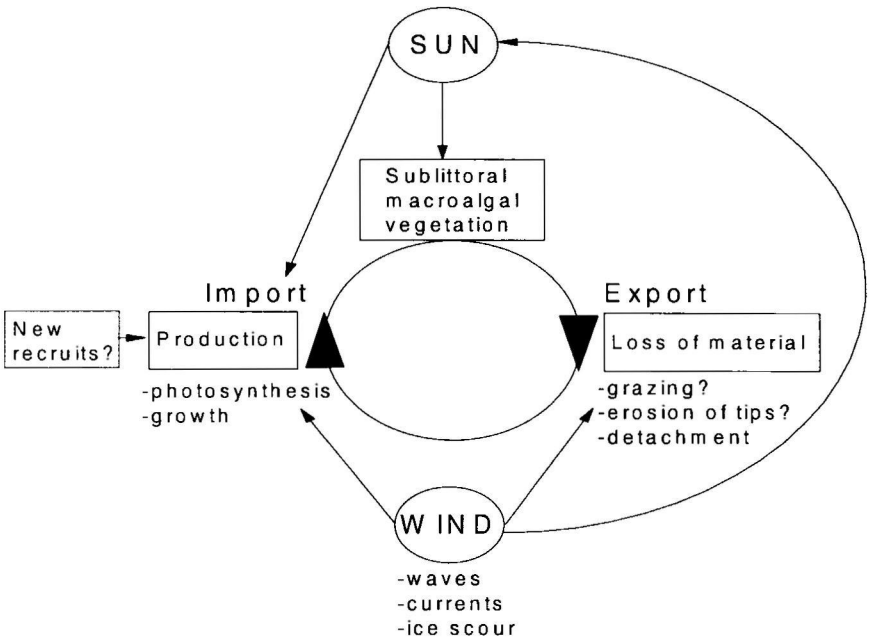

Figure 7.1. Overview of important processes which influence the macroalgal vegetation of Signy Island. Question marks indicate processes which were not studied in this thesis

Environmental conditions

Antarctica is known for the extreme cold temperatures and dark periods in winter The most important environmental factors influencing the presence of macroalgae are salinity, temperature, nutrients and light In Antarctica, the water temperature and salinity are relatively constant, and nutrient levels are generally high in all seasons (**Chapter 6**, Clarke et al 1988) Light is therefore the most important seasonal factor influencing growth and development of the Antarctic macroalgae **Chapter 3** gives the irradiation on the water surface and under water till a depth of 25 m The presence of sea ice has an influence on the underwater irradiance levels Although in winter daylengths are short and sea ice can be present, daily irradiance levels at 25 m water depth reached hardly ever zero values during this study and varied throughout the year between 0 and 0 5 mol m^2 with occasionally higher values In order to increase our knowledge of the behaviour of macroalgae under field conditions, the photosynthetic characteristics of two dominant Phaeophytes, *Desmarestia anceps* and *Himantothallus grandifolius*, and the Rhodophyte, *Myriogramme mangini*, were determined *in situ* and discussed in **Chapter 3, 4** and **5** It is concluded that the macroalgae are very well adjusted to the ambient irradiance levels

Photosynthetic characteristics

The *in situ* measurements of the photosynthesis described in this study confirm that the macroalgae studied can be classified as being shade adapted This was until now only based on studies with cultured species (Wiencke et al 1993) and recently confirmed by Weykam (1996) in laboratory studies on freshly collected material In general, the Antarctic macroalgal species studied till now have a high photosynthetic efficiency (α) and low initial saturating irradiance levels (I_k) and irradiance compensation points (I_c) This field study resulted in general in lower values of the photosynthetic characteristics than found in the cultured individuals Differences can be explained by different measuring techniques and origin of the material Cultured species were grown from sporophytes under continuous irradiance levels and reached several centimetres in length, while in the field experiment adult plants, with lengths of 30 cm for *Myriogramme mangini* and several metres for *Himantothallus grandifolius*, were used under the natural variable irradiance levels

The seasonal variation in irradiance levels found was expressed in the photosynthesis and resulted in seasonality in the photosynthetic characteristics of the macroalgae studied, as well as in the growth of the brown kelp-like macroalga *Himantothallus grandifolius* (**Chapter 3, 4** and **5**) Wiencke (1990) classified the two species *Desmarestia anceps* and *Himantothallus grandifolius* already as "season anticipators", which means that they grow and reproduce in a strategic annual rhythm suitable for the species, triggered or synchronized by daylength, and of which

growth starts in the winter season in response to short days. Information on *Myriogramme mangini* is limited to photosynthetic measurements (Weykam 1996 and this thesis). The species seems to react as a "season responder", which means that growth starts in spring and summer when they experience high light conditions. However, more details about the growth strategy of this species are required (**Chapter 4**).

Growth of Himantothallus grandifolius

Although a year-round study on *Himantothallus grandifolius* has been carried out by Drew and Hastings (1992), their results were limited to shallow depths. At the start of this project, the optimum water depth of occurrence of this species was not known, but later, analyses of the data of biomass and percentage cover gave an optimum of occurrence at 19 m depth (**Chapter 2**). For comparing growth rates of *Himantothallus grandifolius* at different depths, a shallow (12-14 m depth) and deep site (26-28 m depth) were chosen (**Chapter 5**). Laminae at the shallow site were longer and wider than those at the deeper site and grew faster in summer. This can be explained by the higher irradiance levels at the shallow site. In winter, however, the macroalgae showed equal growth rates at both depths. The irradiance level is, therefore, the limiting factor for *Himantothallus grandifolius* to grow at deeper sites. At 25 m water depth an annual irradiance level of 50 mol m^{-2} was reached, while minimum light demands for completion of the life cycle of the Desmarestiales proved to be 31.4 mol m^{-2} (Wiencke 1990). This light level might be the limit for *Himantothallus grandifolius* and restricts this species to water depths where this annual irradiance level occurs. As irradiance levels are highly dependent on the turbidity of the water column, species might occur deeper at places with clearer water (personal observations).

Annual C-budget of the macroalgal vegetation at Signy Island

To estimate a total C-budget of the macroalgal vegetation at Signy Island (Fig. 7.2), the results of the growth measurements of *Himantothallus grandifolius* were used. The total increase in lamina area of *Himantothallus grandifolius* can be determined from Table 5.2a, with which a predicted total lamina area can be calculated (Table 7.1). In combination with the lamina areas at the start of this experiment the percentage loss and growth of lamina material can be calculated for plants growing at the shallow (12-14 m depth) and deep site (26-28 m depth). At the shallow site, a predicted value of 18.1% (± 19.1) of the original lamina area was lost, while at the deep site 3.5% (± 31.0) was gained. It must be kept in mind, however, that the results of this study are restricted to one year and that in other years results will certainly be different. Combining the information available from Table 5.2a and Fig. 2.2, and using a linear regression between growth rate (y) and depth (x) for summer

(y = 9.57 - 0 33 x) and winter (y = 1.83 - 0 04 x), an average net production rate of 91 g C m^2 per year was calculated for *Himantothallus grandifolius* at Outer Island between 2 and 29 m depth. The total biomass of the macroalgal vegetation was 6.3 times the biomass of *Himantothallus grandifolius* (**Chapter 2**), when integrated over the depth interval of 2-29 m. Assuming that the same AFDW/DW ratio can be used for all macroalgae as for *Himantothallus grandifolius*, and that 45% of AFDW is organic carbon, a total macroalgal production of 573.0 g C m^2 per year is calculated for Outer Island. A linear regression (y = 34.93 - 1.07 x) between the percentage loss of material at the shallow (13 m) and gain of material at the deep site (27 m), results in an average loss of 14.3% averaged over 2-29 m depth. This would result in a loss of 81.9 g C m^2 per year (Fig. 7 2), and mean that, based on these data, the macroalgal vegetation at Outer Island could be 3 times as high after one year if not more produced tissue would disappear. Only a small amount of material seems to disappear due to detachement, but for example the bushy macroalgae *Desmarestia anceps* and *Desmarestia menziesii* might be more vulnerable to wind, currents and ice scour Therefore the loss of material is very likely to be underestimated, but at this moment difficult to quantify. In other years the loss of material is probably much higher. It can be expected that over a longer time period the macroalgal community will be in balance. When ice is present or around the island in winter, the water is normally calmer as in the summer period. Most of the macroalgae will therefore be damaged in summer, the same period as productivity is high. In an intensive study by Field and Griffiths (1991) on southern African ecosystems comparable ratios of production-standing stock were found, although the standing stock in their study was 3 times as high as found in this study and detached material was disposed on the beaches and therefore easier to quantify. At Signy Island most of this loose material sinks to hollows of the seabed and decomposes.

Table 7.1. Mean values (± SD) of calculated total area (A), seasonal increase in punched area (A_p), total increase in punched area, predicted total lamina area (total A_p + A_{dec}) and predicted % gain/loss ((predicted total lamina area - A_{oct})/A_{dec}*100) based on the starting values at the shallow (12-14 m, n = 11) and deep (26-28 m, n = 12) site of Outer Island in December of *Himantothallus grandifolius* laminae Area in dm^2, A_{dec} = area in December, A_{oct} = area in October

Site	A	Increase in A_p	Total increase in A_p	Predicted total lamina area	Predicted % gain/loss
Shallow					
Dec	48 3 (33 5)				
April	52 5 (33 7)	5 5 (2 4)			
Oct	47 3 (28 6)	2 7 (2 1)	8 2 (3 6)	56 5 (33 3)	-18 1 (19 1)
Deep					
Dec	18 0 (15 9)				
April	20 0 (13 9)	1 3 (1 2)			
Oct	19 7 (11 0)	1 4 (1 1)	2 7 (1 7)	20.7 (15 8)	3 5 (31 0)

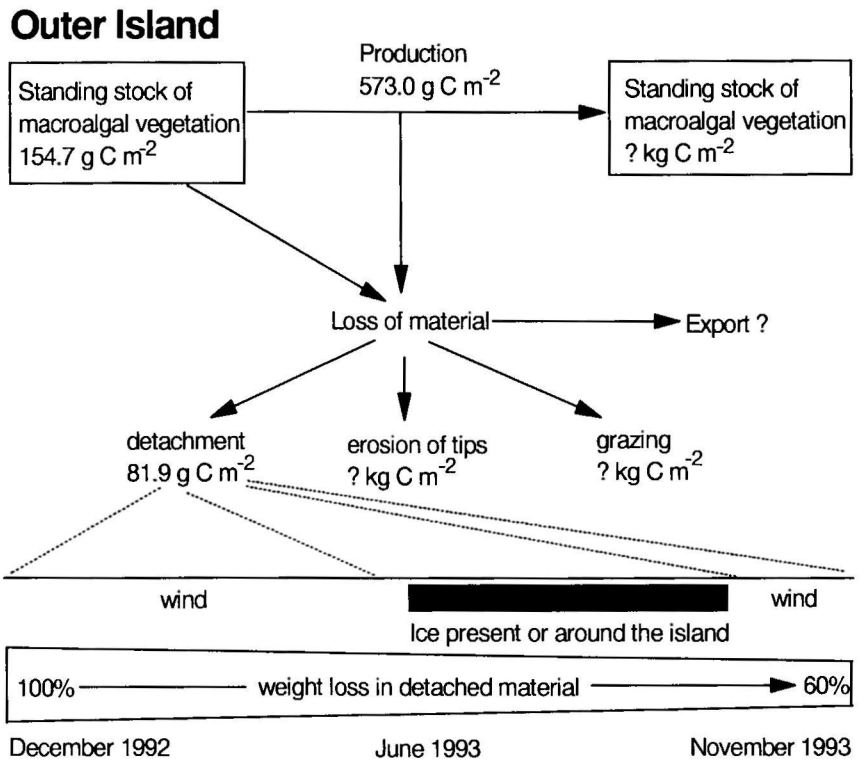

Figure 7.2. C-budget of the macroalgal vegetation at Outer Island, Signy Island (calculated area of macroalgal vegetation from 2-29 m depth is 76,500 m^2). Question marks indicate processes which were not studied in this thesis. Dashed lines indicate the periods of high windspeeds and gales, and where (as a result) most of the detachment of macroalgae occurred

Decomposition of macroalgal material

The amount of detached macroalgae which accumulates on the beaches at Signy Island is negligible compared to the majority which accumulates in hollows of the seabed (**Chapter 6**). Physical decomposition was shown to be more important than microbial decomposition. For *Desmarestia anceps* a weight loss of 40% occurred in untreated material within 313 days (Fig. 6.3), which was mainly caused by fragmentation. Particles disappearing from litter-bags accounted for most of the loss of original tissue. 50,000 kg DW of macroalgal material estimated to be present in a hollow of the seabed of 300 x 200 m (**Chapter 6**), results in 277.5 g C m^{-2}. With a calculated loss of macroalgal material at Outer Island of 81.9 g C m^{-2} per year, the detached material in the hollow is at the most 3 years old when it consists of freshly detached material.

The other cold marine environment: the Arctic

In the Arctic, macroalgae also have to deal with extreme conditions like high variations in irradiance, seasonal changes in daylength and low water temperatures. Contrasting between the two polar areas are the annual irradiance levels and the transparancy of the water column. Henley and Dunton (1995) measured a total annual irradiance level of 45 to 65 mol m^{-2} at a depth of 6-7 m, while at Signy Island these values were determined at a depth of 20-25 m. Antarctic macroalgae also seem to be better adapted to low temperatures than Arctic macroalgal species (Wiencke et al. 1994), because of the different cold water history of the two polar regions. Bischoff-Bäsmann and Wiencke (1996) showed for 15 Antarctic red macroalgae a lower temperature demand for growth than Arctic species. Particularly one endemic species of the Arctic, *Laminaria solidungula*, has been studied intensively (Chapman and Lindley 1980, Dunton 1985, 1990, Dunton and Jodwalis 1988, Dunton and Schell 1986, Dunton et al. 1982, Henley and Dunton 1995). In contrast to the Antarctic kelp-like species, *Himantothallus grandifolius*, this species grows fastest in winter and early spring under thick ice cover when nutrients are available for new tissue growth with light conditions not being optimal (Chapman and Lindley 1980, Dunton et al. 1982). Data on the determination of photosynthetic characteristics of Arctic macroalgae are scarce. *Laminaria solidungula* (Dunton and Jodwalis 1988) in general shows a lower photosynthetic efficiency than *Himantothallus grandifolius*. This might suggest that Antarctic macroalgae are better adapted to lower irradiance levels than Arctic species, but more comparative research between the polar regions is required.

Evaluation of methods used

For description of the zonation patterns both a harvesting and photographic method were used (**Chapter 2**), of which the last method was the less time consuming. With the photographic method a realistic picture of the upper canopy could be made, but the species of the understory were difficult to identify and therefore had to be grouped as Rhodophyta. Information on the understory was obtained from the standing crop data. The harvesting method caused a lot of damage to the environment and macroalgal community. It is therefore advised to use a photographic method as much as possible in studies for describing zonation patterns. The harvesting method has to be used when more specific information on biomass is needed. Patchiness is high in Antarctic macroalgal vegetations and therefore enough replicates have to be sampled.

Primary production in this study was mainly determined by oxygen evolution measurements (**Chapter 3, 4, 5**), while for *Himantothallus grandifolius* also a leaf marking technique was used (**Chapter 5**). The use of ^{14}C was not possible because of the regulations in the Antarctic region and costs which had to be made for the

waste disposal With some assumptions made this method would have given information on something between net and gross photosynthesis (Peterson 1980). At the start of the preparations for the first expedition to Signy Island in November 1991, suggestions made by the personel of the British Antarctic Survey, resulted in the construction of the self-registering incubation chambers Equipment had to be robust, in case seals would try to nibble on it, and should be made in such a way that it could be left in the water for longer time, as diving and boating time was limited. The leaf-marking technique was only applicable, within reasonable time-limits, at the leaf-like macroalga *Himantothallus grandifolius* The leaf-marking method resulted only in information on net production, but one advantage of this method was that the same lamina could be followed in time Both methods used were time consuming, with the marking technique taking more diving time compared to the oxygen evolution technique. In polar waters this can be a crucial factor. One of the disadvantages of the oxygen evolution method involves the use of sophisticated equipment in the field. Usability heavily depends on the weather conditions. Windspeeds above 6 Beaufort stopped the boats to sail without taking needless risks. Therefore, incubations could not always last as long as necessary or had to be postponed for longer time For making seasonal *in situ* P-I curves, the days of measurement should be as closely connected as possible. Several P-I curves during the day should be made first to detect whether P-I curves change during this period. The best results were obtained from macroalgae with small cutting areas and therefore for leaf-like macroalgae, like *Himantothallus grandifolius*, another technique like the marking technique is recommended Unfortunately, not all macroalgae are suitable for applying a marking technique As logistic support might often not be sufficient in polar regions for sophisticated equipment, it is advised in polar waters to use a marking technique when possible and use preferably whole plants instead of parts of plants in incubation chambers

This study adds considerably to the limited *in situ* measurements available on Antarctic macroalgae and contributes to the validation of laboratory studies. Although in other areas of the world macroalgal vegetations are well studied, in Antarctica a lot of areas are still unexplored and basic information (e.g. biomass values) is generally missing. Especially information of macroalgae from high latitudes is lacking, in particular about the photosynthesis of species found by Cormaci et al. (1992) in Terra Nova Bay at 74°31'-74°55'S, where the changes in irradiance levels and length of dark periods are the most extreme. For future protection of this last natural and "clean" area of the world, all possible information on the ecology and distribution of macroalgae, which play an important role in the cycle of life of the Antarctic ecosystem and of the earth, is valuable Recently, the seasonal photosynthetic performance of the endemic Rhodophyte *Palmaria decipiens* has been published (Weykam and Wiencke 1996), and Phaeophyta have been studied under laboratory

conditions (Gómez et al. 1995a, 1995b, Gómez and Wiencke 1996), but in general, studies of Antarctic Rhodophyta are lacking. Also biological interactions like intra- and interspecific competition and predation which shape the structure of littoral communities should be investigated in detail, but this would ask for many years of continuous research.

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Summary

Expeditions to Antarctica date back to the beginning of the 19th century, but gathering information of sublittoral macroalgae remained for a long time restricted to taxonomic studies. Only recently, biogeographical relationships and the ecophysiology of Antarctic macroalgae were studied in laboratory cultures Field observations and *in situ* measurements of primary production of Antarctic macroalgae were generally lacking. Therefore, an intensive study was started in 1990 to determine the number of species present, to collect information of their distribution and zonation pattern and to gain insight in the functioning of some larger Antarctic marine macroalgae under field conditions. At the same time results of previous laboratory studies carried out by other scientists were validated in the field.

The most important environmental factor for Antarctic macroalgae is the ambient irradiance level in the water column. Other factors like salinity and temperature of the water are relatively constant, while the nutrient concentrations are generally high In **Chapter 3** the variance of irradiance levels is given, measured on the surface and under water till a depth of 25 m In summer, with high irradiance levels on the surface, the levels under water are reduced by phytoplankton blooms and sediment being suspended in the water column In winter, however, the water is very clear and between 5 and 10% of the surface irradiance can reach depths of 25 m. When sea ice is present on the water surface, irradiance levels decrease below 2%.

Irradiance levels in the water column, and therefore the water transparency, might play an important role in explaining differences in vegetation at sites of different exposures. In **Chapter 2** the species composition of sample plots of a sheltered site corresponded with plots roughly 1 to 2 meter deeper at an exposed site No relationship was found between the species composition of the algal vegetation and the exposure or the slope of the substratum. The influence of water depth is of course a combination of several environmental factors with irradiance levels as the most important one In this study 36 species were identified. Both species number and macroalgal biomass at Signy Island were low compared with regions of lower lattitudes. The zonation pattern found in this study approached that of the Antarctic peninsula: an ice-abraded zone characterized by the Rhodophyte *Iridaea cordata*, a zone of 5 to 14 m water depth dominated by the Phaeophytes *Desmarestia anceps* and *Desmarestia menziesii* and a zone 15 to 25 m water depth characterized by the large kelp-like Phaeophyte *Himantothallus grandifolius* Earlier studies on depth distribution of macroalgae were mainly based on descriptive and qualitative observations, while in this thesis determination of the zonation pattern is based on biomass and percentage cover data. Depth-response models predicted a

maximum depth of occurrence of 30 and 35 m for *Desmarestia anceps* and *Himantothallus grandifolius*, respectively Deeper than 35 m of water depth the Rhodophytes *Plocamium cartilagineum* and *Pantoneura plocamioides* had high probabilities of occurrence (supported by personal observations).

To increase our knowledge of the oxygen production of Antarctic macroalgae under field conditions, three dominant species were studied in specially developed incubation chambers. In **Chapter 3** the photosynthetic characteristics of *Desmarestia anceps* were studied in different seasons This species proved to be well adapted to low irradiance levels and showed significantly higher photosynthetic capacity and efficiency in spring than in winter or summer. Compared to results from previous laboratory studies, photosynthetic characteristics were lower. Based on annual production rates a maximum depth of occurrence of *Desmarestia anceps* was predicted at 27.6 m. In **Chapter 4** *Myriogramme mangini* proved also to be adapted to low irradiance levels, with a high photosynthetic efficiency (α) and low initial saturation and compensation irradiance (I_k and I_c). The I_k varied significantly between the seasons, and the photosynthetic characteristics were in general lower than found in previous laboratory studies. A maximum depth of occurrence of *Myriogramme mangini* was predicted at 22.9 m depth based on irradiance levels and calculated oxygen production rates. The third species, *Himantothallus grandifolius*, was also adapted to low irradiance levels and showed a seasonal variation in the photosynthetic efficiency (α) and initial saturation irradiance (I_k) (**Chapter 5**). Compared to previous laboratory studies, the results were contrasting, and therefore the use of parts of *Himantothallus grandifolius* in photosynthetic measurements is strongly discouraged. A marking technique, used at the same time for determining growth rates at two different depths, resulted in general in higher production rates compared to the oxygen production method. The higher growth rate at the shallow site compared to the deep site could easily be explained by the higher irradiance levels at shallower depth, but the equal growth rates at both depths in winter could until now not be explained. No satisfying indications were found in chlorophyll *a* or in C, N, P content.

Ice scour, waves and currents detached large amounts of macroalgal material at Signy Island, which accumulated in hollows of the seabed. Decomposition rates (**Chapter 6**) were low and weight loss during 10 months was mainly caused by fragmentation. In this period physical decomposition played a more important role than microbial decomposition.

So far the results indicate that 1) the biomass of Antarctic macroalgae is not negligible and the distribution pattern found is similar as found along the Antarctic peninsula, 2) the macroalgae are very well adapted to the low irradiance levels in Antarctica, show seasonality and have a high photosynthetic efficiency (α) and low initial saturation (I_k) and compensation irradiance (I_c), and 3) decomposition rates are

low.

In **Chapter 7** the results from this thesis are combined and a preliminary annual C-budget is given. Production rates are comparable with southern African macroalgal vegetations, but the estimated loss of material must have been far too low compared to the production rates. In 1993, 573.0 g C m^2 was produced at Outer Island, while only 81.9 g C m^2 was lost again. More compartments of the Antarctic ecosystem have to be studied before a complete C-budget can be given.

Samenvatting

De laatste jaren geniet het Zuidpoolgebied de belangstelling van velen. Niet alleen onderzoekers voelen zich aangetrokken tot dit witte continent, maar steeds meer toeristen zien het Zuidpoolgebied als een laatste uitdaging. Voor de komende 50 jaar is (vastgelegd in het Zuidpool Verdrag) dit laatste onaangetaste stukje aarde veilig gesteld en beschermd tegen verder onderzoek naar grondstoffen, mineralen en tegen een eventueel massatoerisme.

Veel mensen hebben een koud en donker beeld van het Zuidpoolgebied. Toch is er een rijke en gekleurde onderwaterwereld. Reeds lang worden biologische expeditie naar het Zuidpoolgebied uitgevoerd, maar met name het onderzoek naar zeewieren is beperkt gebleven tot het beschrijven van soorten Hiertoe dragen de lage watertemperatuur en de noodzaak van duiken zeker bij. Tegen de verwachtingen van velen in komen zeewieren in grote hoeveelheden voor in het Zuidpoolgebied. De biomassa en het soortenaantal neemt wel af in de richting van hogere breedtegraden. Bij het begin van dit onderzoek was weinig bekend over het functioneren van de zeewieren in de natuurlijke veldsituatie en waren resultaten van laboratoriumstudies nog niet in het veld getoetst Het doel van mijn studie was dan ook inzicht te krijgen in het functioneren van Antarctische zeewieren onder natuurlijke omstandigheden.

Deze studie geeft een gedetailleerd overzicht van de zeewieren die aanwezig zijn in het gebied rond het eiland Signy (South Orkney eilanden). Bestudeerd werd welke soorten voorkomen, in welke hoeveelheden en bedekkingspercentages, hoe produktief de zeewieren zijn gedurende verschillende seizoenen en hoe snel ze afsterven en verdwijnen uit het systeem. Onder water werden in kwadraten (50 x 50 cm) op de zeebodem biomassa en bedekkingspercentages van de zeewieren bepaald, door middel van een destructieve en een fotografische methode. In totaal werden 36 soorten op naam gebracht, 15 meer dan genoteerd in een eerder onderzoek Grote hoeveelheden tot 20 kg nat gewicht per m^2 werden waargenomen van een veel voorkomende soort zoals het bruinwier *Desmarestia anceps*. Een sublitoraal **zoneringspatroon**, vergelijkbaar met dat gevonden langs het Zuidpool-schiereiland, werd beschreven. De bovenste meters van het litoraal waren kaalgeschuurd door het zee-ijs en werden gekarakteriseerd door het roodwier *Iridaea cordata*. Van 5 tot 14 meter waterdiepte waren de bruinwieren *Desmarestia anceps* en *Desmarestia menziesii* in grote hoeveelheden aanwezig, van 15 tot 25 meter domineerde *Himantothallus grandifolius*. Dieper waren voornamelijk de roodwieren *Plocamium cartilagineum* en *Pantoneura plocamioides* aanwezig Via een diepte-respons model werd een maximale diepte van voorkomen van 30 en 35 meter voor respectievelijk de soorten *Desmarestia anceps* en *Himantothallus grandifolius* voorspeld (hoofdstuk 2).

Voor zeewieren zijn omgevingsfactoren zoals zoutgehalte, watertemperatuur, voedingsstoffen en licht belangrijk. In het Zuidpoolgebied zijn de watertemperatuur en het zoutgehalte echter vrijwel constant, en de voedingsstoffen in voldoende mate aanwezig, zodat **licht** de belangrijkste factor is die de groei en ontwikkeling van zeewieren bepaalt. De instraling is erg variabel in het Zuidpoolgebied. Op Signy varieert de daglengte van 19 uur in de zomer tot 6 uur in de winter. De doordringing van licht in de waterkolom varieert ook nog eens door het optreden van een fytoplanktonbloei in de zomer, door sediment dat opwervelt door stormen en golven, maar ook door de ijslaag die in de wintermaanden aanwezig kan zijn. Dit betekent dat de zeewieren goed aangepast moeten zijn aan de daar heersende lichtomstandigheden. Daarom werden fotosynthesekarakteristieken (α, I_k en P_{max}) van drie veel voorkomende zeewieren bestudeerd in onderwaterincubatoren. Hierin werden het zuurstofgehalte, de watertemperatuur en de hoeveelheid licht regelmatig geregistreerd in een datalogger (hoofdstuk 3, 4 en 5). De bestudeerde zeewieren gaan zeer efficiënt om met het fotosynthetisch actieve licht (PAR) dat ze op een bepaalde diepte krijgen, wat blijkt uit hoge fotosynthese-efficiëntie (α) en lage lichtverzadigings- (I_k) en lichtcompensatiepunten (I_c). Geconcludeerd werd dan ook dat de wieren zeer goed aangepast zijn aan de optredende lichtintensiteiten, en gekarakteriseerd kunnen worden als **schaduw-aangepast**. Tot nu toe was dit voor Antarctische zeewieren alleen bestudeerd aan materiaal opgekweekt in laboratoria, maar niet aan levend materiaal ter plekke. Verder bleek dat de zeewieren hun fotosynthesekarakteristieken per seizoen aanpassen, en zijn in het voorjaar de maximale bruto produktie (P_{max}) en fotosynthese-efficiëntie (α) hoger en het lichtverzadigingspunt (I_k) lager dan in andere seizoenen. Om inzicht te krijgen in welke pigmenten precies, en in welke hoeveelheden deze pigmenten een rol spelen bij het omgaan met lage lichthoeveelheden, is meer informatie nodig over de pigmenten die aanwezig zijn in zeewieren van het Zuidpoolgebied.

De **groei** van een wier kan gevolgd worden met behulp van bepaalde methodes. Zo kan het gewicht regelmatig bepaald worden of de toename van het thallusoppervlak, het ontstaan van nieuwe zijtakken etc. De toepasbaarheid van de methode is afhankelijk van de morfologische structuur. Van het blad(lamina)-vormend bruinwier *Himantothallus grandifolius* werd de groei gevolgd door gaatjes van een halve centimeter in het blad te ponsen op een bekende afstand van de basis van het blad (hoofdstuk 5). Dit werd uitgevoerd op een waterdiepte van 12-14 meter en 26-28 meter. De groeisnelheid werd gemeten door de toename in lengte tussen de gaatjes en de toename in breedte van de lamina te bepalen. In de zomer was de groeisnelheid op de ondiepe plek groter dan op de diepe plek. Dit verschil kan verklaard worden door de hogere lichtintensiteiten op de ondiepe plek. Echter, in de winter waren de groeisnelheden op beide dieptes gelijk. Hiervoor kon geen verklaring gevonden worden in het chlorofylgehalte of de C-, N-, P-concentraties. De C-, N-, P- concentraties zouden een indicatie kunnen geven voor meer opslag van reservestoffen in de zeewieren van de diepe plek, maar de resultaten laten

eerder het tegenovergestelde zien Seizoensverschillen in het chlorofylgehalte of de C-, N-, P-concentraties gaven wel een verklaring voor de seizoensverschillen in produktiviteit De hoeveelheid licht schijnt daarom de beperkende factor voor *Himantothallus grandifolius* te zijn op diepere plekken Op 25 meter diepte werd een totaal jaarlijks lichtniveau gemeten van 50 mol m^2, terwijl in een eerdere laboratoriumstudie, voor soorten behorende tot de Desmarestiales, een minimum van 31 4 mol m^2 noodzakelijk bleek voor het afmaken van de levenscyclus Lagere lichtniveau's dan 31 4 mol m^2 zouden limiterend kunnen zijn voor *Himantothallus grandifolius* en het voorkomen van deze soort beperken tot dieptes waar dit lichtniveau aanwezig is Omdat lichtcondities in de waterkolom afhankelijk zijn van de troebelheid, kan *Himantothallus grandifolius* echter dieper voorkomen op plekken met een beter doorzicht (persoonlijke observaties)

Op de ondiepe plek namen de *Himantothallus grandifolius* laminae gedurende de meetperiode van 11 maanden gemiddeld 18 1% af, ten opzichte van de oppervlakte berekend aan het begin van het experiment Op de diepe plek namen de laminae gemiddeld 3 5% toe Met de gegevens van Tabel 5 2a en Fig 2 1 werd, voor *Himantothallus grandifolius* voorkomend bij Outer Island van 2 tot 29 meter diepte, een gemiddelde netto **jaarlijkse produktiesnelheid** van 91 g C m^2 berekend Voor de gehele jaarproduktie van zeewieren voorkomend bij Outer Island, geintegreerd over 2-29 m waterdiepte, was de jaarlijkse produktiesnelheid, 573 0 g C m^2 Het verlies van materiaal werd berekend op slechts 81 9 g C m^2 per jaar, en dit is hoogst waarschijnlijk een onderschatting Rond Signy verdwijnt het meeste van dit materiaal naar de diepere zeebodem

Materiaal dat van de moederplanten wordt losgeslagen door stormen, golven of ijs verzamelt zich rond Signy met name in de diepere delen van de zeebodem In andere gebieden kan het materiaal tevens aanspoelen op de kust, het kan blijven drijven in het water of naar dieptes zinken waar geen licht meer is (hoofdstuk 6) In dit onderzoek werd ook de **decompositie** van losgeslagen wieren bestudeerd Vooral in het eerste jaar bleek fysische decompositie een grotere rol te spelen dan microbiele decompositie De snelheid van de microbiele decompositie van zeewieren van de Zuidpool en het beschikbaar komen van de voedingsstoffen voor het kust- en diepwatersysteem zijn tot nu toe onbekend

Zeewieren hebben in het **Noordpoolgebied** te kampen met dezelfde extreme omgevingsfactoren als in het Zuidpoolgebied grote variaties in licht, seizoensveranderingen in daglengte en lage watertemperaturen De helderheid van het water rond de Noordpool kan op vele plekken slechter zijn dan die van het Zuidpoolgebied Jaarlijkse lichthoeveelheden gemeten op 6-7 meter diepte in het Noordpoolgebied komen overeen met jaarlijkse lichthoeveelheden gemeten op 20-25 meter rond Signy Zeewieren van het Zuidpoolgebied lijken beter aangepast te zijn aan de lage watertemperaturen dan die van het Noordpoolgebied en hebben

een lagere temperatuur voor hun groei nodig. Een verklaring kan gevonden worden in het verschil in "koudwatergeschiedenis" van de twee poolgebieden. De temperaturen van het zeewater in de Zuidelijke oceaan zijn reeds gedurende 14 miljoen jaar zeer laag, terwijl op het Noordelijk halfrond de watertemperaturen slechts 3.5 miljoen jaar laag zijn. In het Noordpoolgebied is voornamelijk *Laminaria solidungula* bestudeerd, die in tegenstelling tot *Himantothallus grandifolius* het hardst groeit in de winter en het vroege voorjaar onder een dikke ijslaag, en tevens een lagere fotosynthese-efficiëntie (α) bezit dan *Himantothallus grandifolius*.

Van de tijdens deze studie toegepaste **methoden**, om het zonatiepatroon en de produktie te bestuderen, blijken in het Zuidpoolgebied de fotografische methode (hoofdstuk 2) en de bladmarkeringsmethode (hoofdstuk 5) het beste bruikbaar te zijn (deze laatste echter alleen voor bladvormende zeewieren). De fotografische methode werd gebruikt om het zonatiepatroon vast te leggen en was minder tijdrovend dan de destructieve methode. De destructieve methode, waarbij materiaal wordt verzameld, is zeer vernietigend voor de omgeving, en kon bovendien vanwege de kou niet intensief genoeg worden uitgevoerd. Daarom wordt deze methode voor polaire gebieden afgeraden. Voor *Himantothallus grandifolius* bleek de bladmarkeringsmethode het beste bruikbaar voor het bepalen van de produktie in vergelijking met de zuurstofevolutiemethode. Ondanks het feit dat de bladmarkeringsmethode de meeste duiktijd kost werden relatief betrouwbare resultaten verkregen. In het algemeen werd met de zuurstofevolutiemethode een beter resultaat verkregen bij wieren met een kleine thallus-doorsnede. Bij slechte weersomstandigheden was een bemonsteringsdag voor de zuurstofevolutiemethode verloren, en moesten incubaties worden ingekort of worden afgelast. Bovendien moesten de incubaties in een zo kort mogelijke periode worden uitgevoerd, wat door weersomstandigheden of ijscondities vaak niet mogelijk was. In het algemeen wordt bij de zuurstof-evolutie methode geadviseerd om complete planten te gebruiken en eventueel grotere incubatiekamers te ontwerpen. Tevens wordt aangeraden zoveel mogelijk metingen uit te voeren. De logistieke ondersteuning zal in polaire gebieden vrijwel altijd onvoldoende zijn, zodat om die reden een markeringsmethode geadviseerd wordt. Helaas zijn niet alle zeewieren geschikt om een markeringsmethode op toe te passen. Dit zal één van de redenen zijn waarom zo weinig metingen naar de groei van zeewieren in het veld zijn uitgevoerd. Tevens verklaart dit waarom de gegevens van het Noordpoolgebied beperkt zijn tot één *Laminaria* soort.

Dit promotie-onderzoek draagt bij tot een betere **kennis** van de zeewieren voorkomend op de rotskusten van het Zuidpoolgebied en dan voornamelijk in de veldsituatie. Toch zijn veel gebieden nog onbekend en is zelfs basale informatie vaak niet voorhanden. Vooral informatie over zeewieren voorkomend op hogere breedtegraden, waar de veranderingen in licht en daglengte nog extremer zijn,

ontbreekt. Met name de informatie over roodwieren, zowel op inter- als intra-specifiek niveau, en informatie over biologische interacties en begrazing is zeer beperkt.

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Curriculum vitae

Patty Brouwer werd geboren op 21 februari 1964 te Heerlen. In 1982 behaalde zij op de Scholengemeenschap Sintermeerten in Heerlen het diploma Atheneum-B, waarna aansluitend de studie Biologie aan de Katholieke Universiteit te Nijmegen (KUN) werd gevolgd. Een hoofdvak werd uitgevoerd bij de afdeling Aquatische Oecologie op de KUN, met een stage van 9 maanden op het Nederlands Instituut voor Oecologisch Onderzoek, Centrum voor Estuariene en Mariene Oecologie (NIOO-CEMO) te Yerseke, en een scriptie-onderzoek van 3 maanden aan de Universiteit van Cork (Ierland). Een bijvak werd gevolgd bij de afdeling Experimentele Plantenoecologie van de KUN. Daarnaast werd een cursus didactiek van 2 maanden gevolgd, met praktijkervaring op het Boschveld College te Venray. Tevens vervulde zij verschillende studentassistentschappen. In september 1989 behaalde zij de titel van doctorandus. Vanaf februari 1990 tot januari 1991 was zij werkzaam als wetenschappelijk onderzoeker op het NIOO-CEMO. Aansluitend was zij tot februari 1995 werkzaam als Onderzoeker in Opleiding (OIO) bij de Nederlandse Organisatie voor Wetenschappelijk Onderzoek en gestationeerd op het NIOO-CEMO te Yerseke. Het onderzoek verricht gedurende de periode vanaf februari 1990 omvatte twee expedities van respectievelijk 5 en 14 maanden naar Signy Island, South Orkney Islands, Antarctica, en staat beschreven in dit proefschrift. Deelgenomen werd aan congressen over Antarctisch onderzoek in Bremen (Duitsland), Venetië (Italië) en Veldhoven, en aan een phycologisch congres in Keulen (Duitsland). Na afloop van het OIO-contract is zij als vrijwilligster doorgegaan op het NIOO-CEMO met de uitwerking en rapportage van het promotie-onderzoek en heeft zij haar proefschrift voltooid. In juli 1996 heeft zij als post-doc op een EC-project een positie aanvaard als wetenschappelijk onderzoeker bij het NIOO-CEMO. Doel van dit onderzoek is het bestuderen van de invloed van UV-straling op zeewieren in het Noordpoolgebied.

Sponsors

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